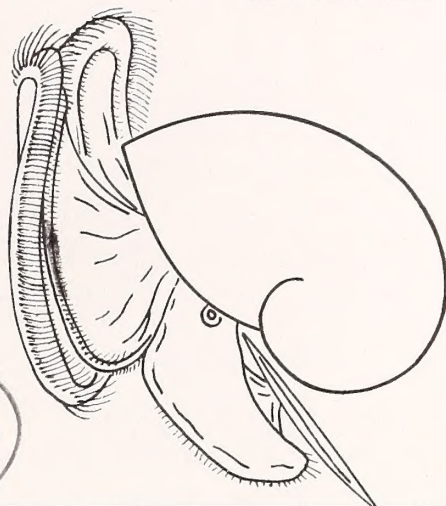
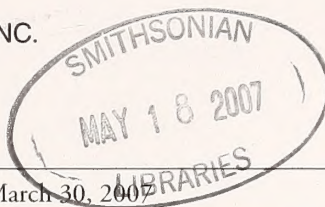


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Population Dynamics and Reproduction of a *Musculium argentinum* (Bivalvia: Sphaeriidae) Population in Southern Chile, South America

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Abstract. The aim of the present study was to provide data about the population dynamics and reproductive traits of a *Musculium argentinum* (d'Orbigny, 1835) population inhabiting a channel next to the city of Lautaro in southern Chile. Results showed that *M. argentinum* size population structure varied during the study period, with brooding adults present throughout the year, with the highest frequencies in December 2002, and March, August and September 2003, producing offspring throughout the year. The smallest specimen brooding was 2.6 mm collected in May 2003 and the size of population first brooding corresponded to the 3.0–3.9 mm class size, collected in March 2003. *M. argentinum* at the study site is an ovoviviparous, iteroparous, sequential brooder, producing offspring throughout the year. These characteristics are attributed to the stable habitat.

INTRODUCTION

Sphaeriid clams are cosmopolitan and ubiquitous in their distribution. They are filter feeders and often play an important role in the dynamics of nutrient and energy cycling in freshwater bodies, i.e., streams and ponds (Wallace et al., 1977). Despite this importance in aquatic environments, relatively little is known about the life histories of sphaeriid clams, especially those from the Southern Hemisphere.

While the majority of marine bivalves are oviparous, with some notable exceptions (Mackie, 1984; Brusca & Brusca, 1990; Ponder, 1998) most freshwater bivalves, including families of the order Unionoida and the two veneroid families Sphaeriidae and Corbiculidae exhibit ovoviviparity and viviparity to various degrees.

Evolutionary aspects of the reproductive biology have been studied in limnic molluscs and put in a phylogenetic context in naiad bivalves (Unionoida) (Dillon, 2000; Graf, 2000; Graf & Ó'Foghil, 2000; Hoeh et al., 2001; Schwartz & Dimock, 2001); in finger nail clams and pill clams (Sphaeriidae) (Heard, 1977; Cooley & Ó'Foghil, 2000; Mansur & Meier-Brook, 2000; Korniuschin & Glaubrecht, 2002). Studies conducted with freshwater clams, from the family Sphaeriidae provide an interesting perspective, since these clams are found in widely varying habitats. This is specially true for *Musculium*, which inhabits both permanent and temporary water bodies in the Northern Hemisphere, and which show differences in their reproductive traits, such as number of generations per

year, braditictic or tachytictic reproductive pattern among others.

Sphaeriidae is one of two families of freshwater bivalves represented in Chile (Parada & Peredo, 2002). The first record of *Musculium argentinum* (d'Orbigny, 1835) in continental Chilean waters was reported by Sobarzo et al. (2002). In view of the great variability in reproductive function and life cycles exhibited by *Musculium* populations inhabiting various habitats and the scarce, almost nonexistent studies on Sphaeriidae life cycles from the Southern Hemisphere, in South America in particular, in the present study, some aspects of the population dynamics and reproductive traits of a population of *M. argentinum* inhabiting a permanent freshwater body in the Southern Hemisphere, are described and compared with those of other populations of *Musculium* from the Northern Hemisphere.

MATERIALS AND METHODS

Musculium argentinum were collected monthly from September 2002 to September 2003 from the bank bed of a permanent channel which flows out from the Cautín river, next to the city of Lautaro, southern Chile (38°32'S; 72°27'O). At this point the channel is approximately 2 m wide, 0.2–0.6 m deep and has a moderately fast water flow (surface velocity of 0.2 m sec⁻¹). Most of the substrate at the collection site is composed of mud. Mean water temperature varied from 9.5°C in winter to 15°C in summer. The water is well-oxygenated (>77% saturated throughout the year) and a mean pH near neutrality (6.7). Samples were collected at random with a 15 × 10 cm standard grab,

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and specimens sifted through 1.0 mm sieves. Samples consisted of >100 clams.

Soft tissues of 10 individuals were histologically processed for light microscopy and examined to determine sex and gonad structure.

To determine the monthly population size structure of *Musculium argentinum*, the shell length (anterior to posterior dimension) was measured to the nearest 0.5 mm with a digital caliper for clams >2 mm long and with a stage-mounted micrometer under a dissecting microscope for clams <2 mm long.

Biometric parameters were determined and the following correlations defined: valve length (VL) vs. valve height (VH), VL vs. valve width (VW) and VL vs. specimen weight (SW).

To assess the reproductive status of the population, approximately 60 adults from each monthly sample were dissected to examine for the presence of embryos. From 8 adults, intramarsupial embryos were removed from each brooding sac in the inner demibranchs, and extramarsupial embryos in the mantle cavity, were counted and measured (length) to the nearest 0.01 mm with a stage-mounted micrometer (Wolfe 10 \times) under a dissecting microscope.

During 2002 spring months (November and December) and 2003 fall months (April and May) 18 brooding adults of sizes representative of the population were processed to estimate the number and size of intramarsupial and extramarsupial embryos. For intramarsupial embryos, four size classes were established: C1: 0.1–0.30 mm; C2: 0.31–0.6 mm; C3: 0.61–0.9 mm and C4: 0.91–1.2 mm. For extramarsupial embryos, all were larger than 1.21 mm. The smallest individual with embryos and the smallest size class with equal or less than 50% of individuals brooding were determined each month.

RESULTS

Population Dynamics

The size of the specimens found during the study period ranged from 2.6 to 10.1 mm. The valve height (VH) ranged between 8.4 and 2.2 mm; valve width (VW) between 5.5 and 2.7 mm and wet weight between 5 and 21.6 mg. The biometric correlations VL vs. VH ($R^2 = 0.9171$), VL vs. VW ($R^2 = 0.8656$) and VL vs. VW ($R^2 = 0.8277$) are highly significant. The relation VL vs. number of brooding sacs in adults is not significant.

Monthly variations in adult population size structure between October 2002 and September 2003 did not show a definite tendency. However, small individuals (2.0–2.9 mm) were collected during December 2002, May, August and September 2003 (Figure 1).

Juveniles (<2 mm) were observed in November 2002, February, and May 2003 and in less abundance

in December 2002, August and September 2003 (Figure 2).

Reproduction

Gonadal organization is shown in Figure 3. Male and female gametes can be seen within gonadal follicles. Male gametes are more abundant than female ones. Hermaphrodite individuals brood their embryos in the inner demibranchs. Monthly records show that more than 20% of adults have embryos in the brood sacs throughout the study period, reaching values close to 50% in December 2002, March, August and September 2003 (Figure 2).

Monthly records of brooding adults (18 individuals examined monthly) showed that the number of brooding sacs is variable, ranging from two to eight sacs in both inner demibranchs per individual, five being the maximum number of brooding sacs found in a single demibranch. There is no significant correlation between the number of brooding sacs and the size of adults (Figure 4).

The size of brooding sacs in an inner demibranch in the same individual is variable. The largest sac observed was 3.3 mm long and 1.8 mm wide. The smallest one was 0.57 mm long and 0.39 mm wide. Both values were registered in an adult 9.4 mm length in November 2002.

Table 1 shows data of number and size of intramarsupial and extramarsupial embryos from the brooding adults processed during spring 2002 (November and December) and fall 2003 (April and May). Results show that all brooding adults have sacs at different developmental stages. In individuals, the size of embryos within the same sac is almost the same. However, the size of embryos varies between brooding sacs showing that one adult is brooding embryos at different developmental stages simultaneously.

The smallest specimen with embryos (individual first brooding) observed was 2.6 mm in a specimen collected in May 2003. The smallest size class with more than 50% of brooding individuals was 3.0–3.9 mm in specimens collected in December 2002 (66.7%), March 2003 (100%) and July 2003 (80%).

DISCUSSION

The absence of correlation between valve length and number of brooding sacs observed, has been explained by the physical arrangement of offspring. Size limited brood capacity is common among species with hard exoskeletons such as molluscs (Bayne et al., 1983; Callow, 1983). Beekey & Hornbach (2004) reported in *Sphaerium striatinum* that brood size is constrained by the physical arrangement of offspring and the retention of extra-marsupial offspring. In *M. argentinum*, ab-

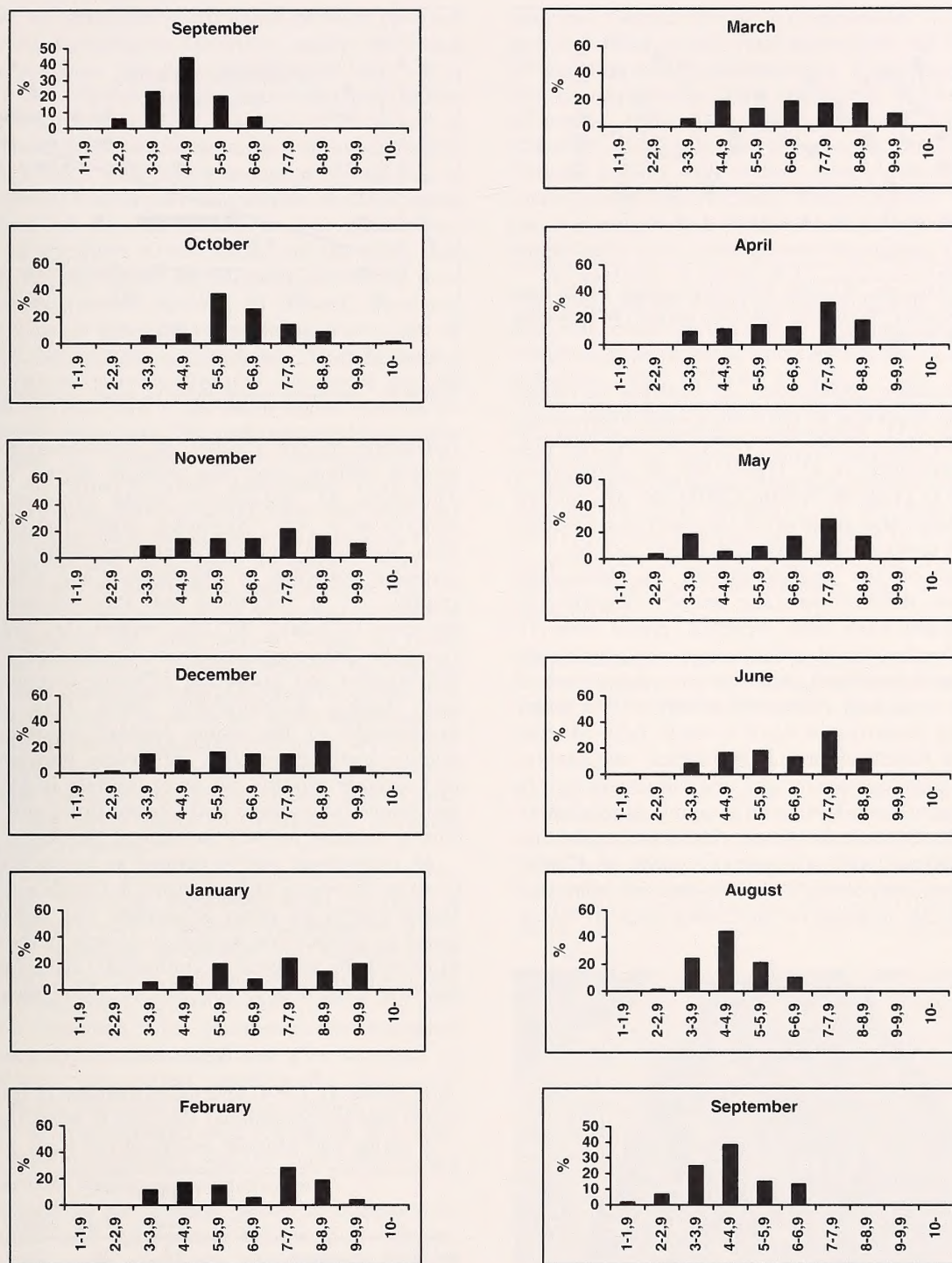


Figure 1. Monthly size structure of *M. argentinum* population at the study site during the study period.

sence of correlation between valve length and number of brooding sacs, can be explained just by the arrangement of offspring. (Table 1).

Like all Sphaeriids, *M. argentinum* is a simultaneous

hermaphrodite and incubates eggs in the inner demi-branches within marsupial or brooding sacs. Our results indicate that the population dynamics of *M. argentinum* at the study site differs from that reported for

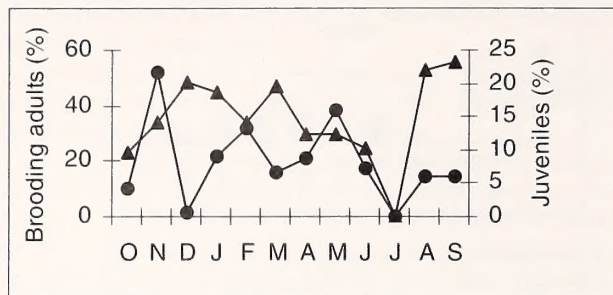


Figure 2. Monthly variation (%) of brooding adults and juvenile frequency (%) during the study period (▲: brooding adults %; ●: juveniles %).

other *Musculium* populations. In contrast to results reported by Mackie et al. (1976) in a *Musculium securis* (Prime) population, Morton (1985) for *M. lacustre*, Müller, Hornbach et al. (1991) for *M. partumeium* (Say) and O'Toole & Wilson (2001) for *M. lacustre* among others. *M. argentinum* at the study site, presents adults and juveniles throughout the study period.

In most of the studies carried on *Musculium* populations, definite spawning periods (juveniles or larvae release) have been reported, giving birth to cohorts. Hornbach et al. (1982) report two generations of clams were produced each year in a population of *Sphaerium striatinum* (Lamarck) in Ohio, with major recruitment occurring in April to early July. Morton (1985) and Hornbach et al. (1991) report two generations in a year (one spring and one fall generation) in *M. lacustre* in Hong-Kong and in ponds in Minnesota respectively. O'Toole & Wilson (2001) point out that *M. lacustre* produces just one generation in Citadel Pond, Dublin. Mouthon (2004) reports two spawning periods in *M. lacustre* in the Saône river at Lyon.

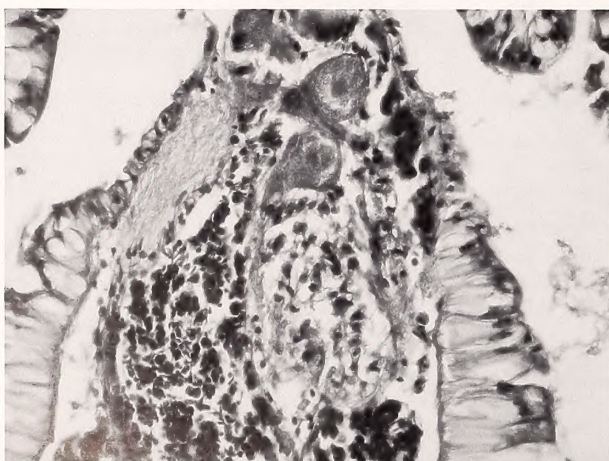


Figure 3. Microscopic organization of the gonad of *M. argentinum* showing the male (M) and the female (F) portion. $\times 1000$.

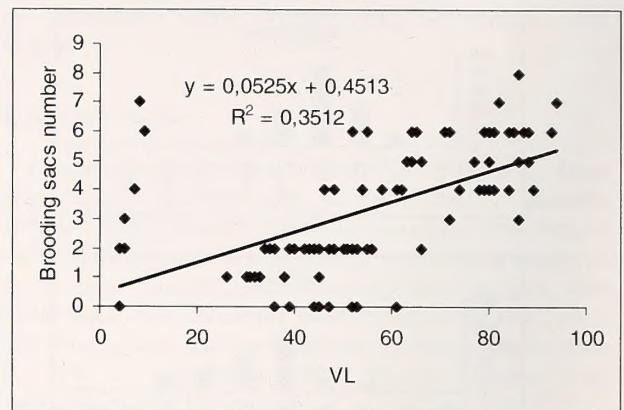


Figure 4. Brooding sacs number vs. adult valve length (mm).

According to our results, *M. argentinum* does not present definite spawning periods during the year. Therefore, *M. argentinum* would originate several cohorts in a year, November 2002, February, and May 2003 being the months with the highest number of juveniles collected in the substratum which were smaller, or of the same size than extramarsupial embryos (< 2 mm). In this respect *M. argentinum* resembles *Sphaerium striatinum*, reported as a sequential brooder and producing offspring throughout the year (Beekey & Hornbach, 2004). This could be attributable to the stable habitat conditions, i.e., relative small temperature differences between winter and summer months, no great changes in hydrologic conditions (abundance and current flow) and in food supply (organic matter) throughout the year.

M. argentinum can be defined as ovoviviparous, in contrast to reports of Korniushev & Glaubrecht (2003), Hetzel (1993) for other Sphaeriids. Our definition is based on the fact that we did not observe in the sections examined the presence of epitheloid cells- functional nutritive structures in the wall of brood sacs or any

Table 1

Size classes (C1–C4) and mean member of intramarsupial and extramarsupial embryos in brooding adults in spring and summer month of the study period.

	Spring 2002		Fall 2003	
	Nov	Dec	April	May
Adults n° processed	18	24	18	12
Adults size range (mm)	4.6–9.4	3.7–8.9	3.4–8.6	3.2–8.1
Mean number embryos: intramarsupial				
C1 (0.1–0.3 mm)	2	2.8	10.7	7.1
C2 (0.31–0.6 mm)	6.6	4.1	6.6	8.0
C3 (0.61–0.9 mm)	8.0	6.1	4.0	4.6
C4 (0.91–1.3 mm)	0.5	0.3	1.7	4.6
extramarsupial (> 1.31 mm)	3.4	0.3	1.6	2.1

other cell or structure which could provide parental nutrients to the embryos. Therefore, embryo brooding in *M. argentinum* just provides parental care, so in a strict sense, this corresponds to ovoviviparity as has been reported for the great majority of Sphaeriids in agreement with Mackie's definition of ovoviviparity (Mackie, 1978). It is in disagreement with Meier-Brook (1970), Hetzel (1993) and Korniusshin & Glaubrecht (2003) and others, who point out that Sphaeriidae qualify for the term eu-viviparous, on the basis that nutrients for embryonic development are mainly provided by the parental animal. At present, from our point of view, in Sphaeriidae and in *M. argentinum* in particular, the nutrition of embryos depends on the yolk stored in oocytes. Despite the small size of sphaeriid oocytes, due to the small size of specimens, including *M. argentinum*, the yolk contained in oocytes is sufficient to sustain embryo development. In addition, eu-viviparity would correspond to an anatomic connection between embryonic and maternal tissues, giving origin to the placenta, as present in some fishes, reptiles and mammals. Viviparity could be defined as when, in addition to parental care, embryo nutrition is provided by the parental animal by mean of secretory cells or any other way in which no tissue connection is involved. Posterior electron microscopy studies might clarify the nature of embryo nutrition in *M. argentinum*. *M. argentinum* has direct development, giving birth to small individuals (<2 mm). We did not observe any developmental stage that could correspond to a larval stage as reported by Hetzel (1993) who describes five larval stages in *M. lacustre* including sexually mature larvae.

The presence of brooding sacs in the inner demi-branches in the same individual with embryos in different development stages in *M. argentinum* corresponds to sequential brooding and represents an evolutionary progress of parental care, from synchrony without brood sac, synchrony with brood sac and sequential brooding with ontogenetically staggered brood sacs and brooded juveniles. This sequence of parental care may reflect selection for accelerated oogenic cycles, and early maturation which is a characteristic of several sphaeriid taxa (Cooley & Ó'Foghil, 2000). This is in accordance with the small size at which *M. argentinum* reaches sexual maturation.

M. argentinum has a small gonad as compared to Corbiculidae and *Eupera* and *Byssanodonta*, (Euperinae) which is in agreement with Dreher Mansur (1993). Examination of gonad sections revealed that the male portion of the gonad was at a more advanced stage of maturation than the female portion, which agrees with reports of Morton (1985) in *M. lacustre*. These observations differ from Mackie et al. (1976) who reported protogyny in *M. securis*, and who described gonads devoid of gametes during winter

months. Despite the earlier maturation of the male portion of the gonads, final maturation and evacuation of gametes occur simultaneously. Simultaneous maturation of gametes also occurs in *M. partumeium* (Thomas, 1959) and *Sphaerium simile* (Say, 1817) (Zumoff, 1973). Within Sphaeriidae, *M. argentinum* showed gonads with mature gametes throughout the study period which included winter months. Therefore, *M. argentinum* is a simultaneous or functional hermaphrodite with active gonads throughout the year.

The presence of adults of *M. argentinum* throughout the study period which produce offspring throughout the year, could be indicative of iteroparity instead of semelparity as reported for other species of *Musculium* (Morton, 1985; O'Toole & Wilson, 2001; Mouthon, 2004). Our data therefore indicate the great variation in life history exhibited by Sphaeriids. This variation is determined by environmental conditions, reflecting a plasticity which has contributed to their cosmopolitan distribution. This variability in life history makes interpopulation comparisons difficult to interpret and also raises the probability that life cycles of many other species might be more variable than is at present appreciated.

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A New Deep-Water Species of the Genus *Epilepton* (Bivalvia: Galeommatoidea) from the Atlantic

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Abstract. A new species of the genus *Epilepton* is described from the Atlantic. This is the first species of the genus to be described from abyssal depths. Described species of the genus that occur in the Atlantic are listed, and the relationship between *Epilepton* and *Neolepton* is discussed.

INTRODUCTION

Species of the Galeommatoidea have been described mostly from shallow waters (e.g., Dall, 1899; Popham, 1940; Chavan, 1959; Boss, 1965; Ponder, 1971; Morton & Scott, 1989; Aartsen, 1996a and b; Salas & Gofas, 1998; Giribet & Peñas, 1998). Recent sampling by American research vessels in the Atlantic has shown that they also occur at abyssal depths (Allen, 2000) (see Allen & Sanders, 1996, for description of the extent of these studies). Many of the described species are either commensal or epiparasitic. The species described here is sub-trapezoidal in shape and resembles *Epilepton subtrigonum* (Jeffreys, 1875) from the West European Basin, and a Mediterranean species *Lepton solidulum* (Gaglioni, 1991).

The name *Epilepton* was introduced by Dall (1899) without explanation. *Epilepton*, together with *Neolepton* Monterosato, 1875, *Lutetina* Vélain, 1876, and *Planikellia* Cossmann, 1887, were listed by Dall (1899) as subgenera of *Lepton* in the family Leptonidae. Again, no reason was given for this. Later, *Epilepton* and *Neolepton* were included in the family Neoleptonidae by Theile (1935) and which he included within the Cyamacea. Thereafter, this arrangement was followed by most authorities (Bowden & Heppell, 1968) until recently, *Epilepton clarkiae* (Clark, 1852) and a new species of *Epilepton* (*E. parrussetensis* Giribet & Peñas, 1998) were included in the Montacutidae (Salas & Gofas, 1998). In transferring *Epilepton* to the Montacutidae Salas & Gofas (1998) followed Deroux (1961). Heppel (1964) and Bowden & Heppell (1968) had dismissed Deroux's opinion as fallacious. Nevertheless, the hinge and mantle of described species of *Epilepton* differ from those of *Neolepton* (see Salas & Gofas, 1998 and Allen, 2000) and are similar in most respects to montacutid species described by Popham (1940) and Morton & Scott (1989).

Genus *Epilepton* Dall, 1899

Type species by monotypy: *Lepton clarkiae* Clark, 1852

Shell small (<3 mm total length), fragile, equivalve and somewhat compressed, inequilateral, anteriorly extended, ovate or subtrapezoidal, with maximum length ventral to mid-height giving a somewhat dorsally angulate appearance. White or pale fawn in colour, with fine irregular commarginal growth lines and, in some species, faint radial lines. Hinge plate with elongate anterior and posterior lateral teeth in each valve, single slightly oblique cardinal tooth anterior to umbo in each valve, the left cardinal usually smaller than right. Internal ligament, ventral and posterior to umbo, with a fine, barely visible external ligament present in some species. Anterior mantle margin of pedal aperture with sensory papillae.

The following Atlantic species are recognized:-

Epilepton clarkiae (Clark, 1852)

Figs. 1b & 5c

Type locality: Coralline zone off mid-south coast Devon, UK

Type material: Syntypes, U.S. National Museum 199440

Lepton clarkiae Clark, 1852: 191

Epilepton clarkiae, Dall, 1899: 876

Epilepton clarkiae, Tebble, 1966: 87, figures 41a–c

Epilepton clarkiae, Bowden & Heppell, 1968, 248, 266

Epilepton clarkiae, Nordsieck, 1969, 89, plate XIV, figure 50.70

Lepton clarkiae, Warén, 1983: 163, plate 8, figures 1 and 2

Epilepton clarkiae, Aartsen, Menkhurst & Gittenberger, 1984: 65, figure 330

Epilepton clarkiae, Aartsen, 1996: 32, 36, figure G

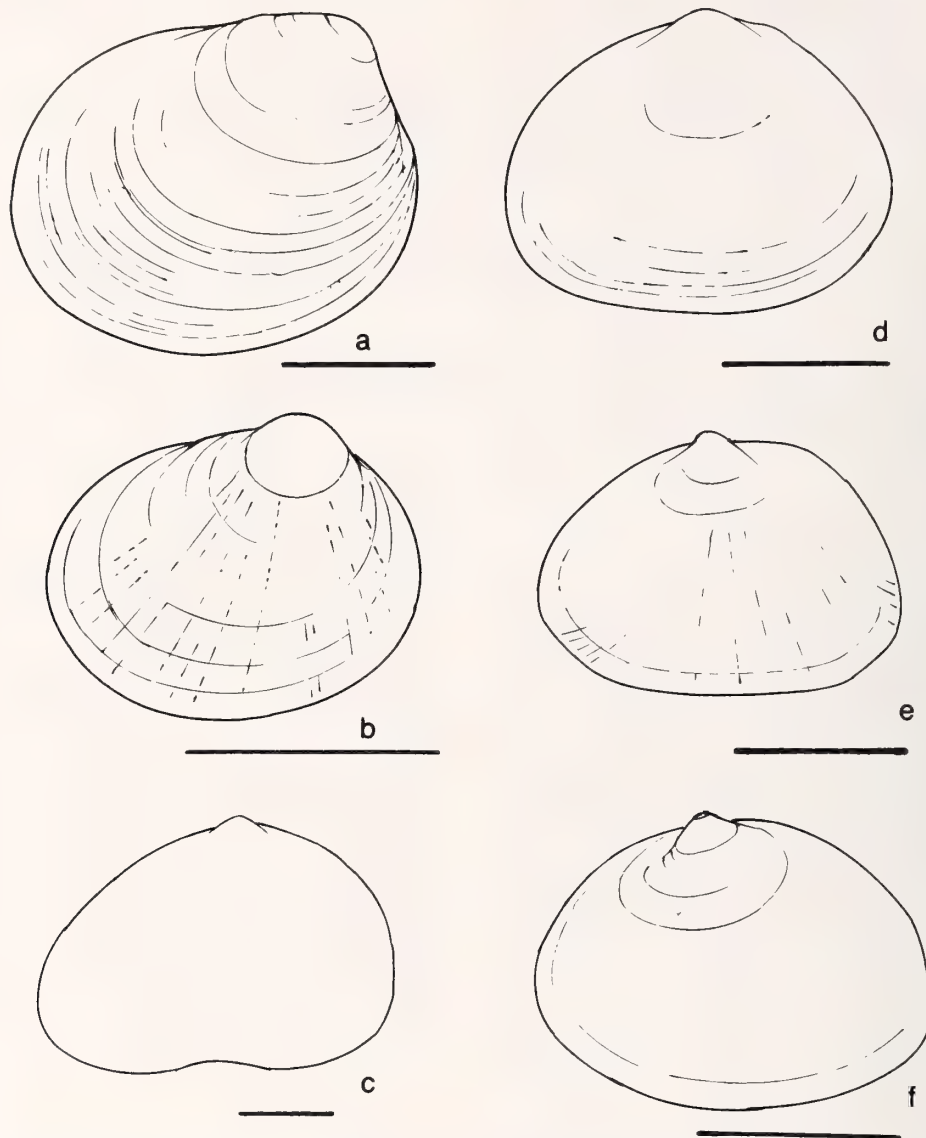


Figure 1. Species of *Epilepton*. Lateral views of the left valves of a, *E. parrussetensis*; b, *E. clarkiae*; c, "*Potidoma subtrigonum*"; d, *E. solidulum*; e, *E. elpis*; f, *E. subtrigonum*. Scale bars = 1 mm.

Epilepton clarkiae, Salas, 1996, 62

Lepton clarkiae, Salas & Gofas, 1998: 69

Epilepton clarkiae, Delongueville & Scaillet, 1999: 29

Distribution: Southwest European Basin and Mediterranean, upper shelf.

Epilepton parrussetensis Giribet & Peñas, 1998

Fig. 1a

Type locality: off Vallcarca (Sitges, Barcelona, 41°06'59"N 1°54'23"E), 250–350 m

Type material: Holotype, MNHN 15.07/4644. Paratypes, MNHN and BMNH

Epilepton parrussetensis Giribet & Peñas, 1998: 118, figures 1–4

Distribution: Northwest Mediterranean, from shelf to upper slope depths.

Epilepton solidulum (Gaglini, 1991)

Fig. 1d

Type locality: off Cape Palermo, 90 m

Type material: Holotype, Museo Civico di Zoologia di Roma

Lepton solidulum, Monterosato, 1875: 12

Lepton solidulum, Monterosato, 1878: 68

Lepton solidulum Gaglini, 1991: 176, figures 189 and 190

Lepton solidulum, Aartsen, 1996a: 34, figure F (left photograph)

Distribution: West European Basin and Mediterranean, from shelf to upper slope depths.

Remarks: Monterosato (1875, 1878) listed a considerable number of bivalve species, some of which he recorded as nov.sp., but without description. Recently, a number of his *nomina nuda* have been briefly described and figured by Gaglini (1991), thus making them available for the first time. Included is *Lepton solidulum* regarded by Gaglini (1991) as a valid species. This species was also doubtfully recorded by Aarstsen (1996b) and photographed but wrongly identified by him as *Hemilepton nitidum* (Turton, 1822) (Aartsen, 1996a fig. F, left hand photograph). Although the shell is trapezoidal as compared the more ovate shape of *E. clarkiae* and *E. parrussetensis* (figure 1) the basic structure of the hinge is the same.

Epilepton subtrigonum (Fischer, 1873)

Figs 1f & 5a

Type locality: Fosse de Cape Breton, Biscay

Type material: Syntypes labelled *Lepton* n.sp.B of Biscay, Folin, U.S.National Museum 199475

Cited specimen: deposited in the Muséum d'Histoire Naturelle, Paris

Lepton subtrigonum Fischer, 1873, ex Jeffreys ms: 82, plate 2, figure 10

Lepton subtrigonum, Cerulli-Irelli, 1908: 2, plate 1, figures 5a and b

Lepton subtrigonum, Warén, 1980: 47

Material: Thalassa, station z425, 48°27.9'N 09°44.0'W, 700 m., 1 spec.

Distribution: Mid-slope depths in West European Basin.

Shell description: Very small <3 mm total length, subtrapezoidal (length/height ratio: 1/0.72), slender (length/width ratio: 1/0.41), equivalve, slightly inequilateral, umbo anterior to midline, white, translucent, almost invisible very fine, closely packed concentric striae, dorsal margin close to umbo almost straight and parallel to mid-ventral margin, antero-dorsal margin

oblique and shallowly curved, postero-dorsal margin more convex, both anterior and posterior shell limits ventral to mid-horizontal axis, mid-ventral margin almost straight or very slightly convex; umbos small, inwardly turned; hinge-plate broad, each valve with elongate posterior and anterior lateral teeth, small cardinal tooth in each valve; triangular internal ligament posterior to cardinal tooth, elongate opisthodontic submarginal external ligament hardly visible externally.

Remarks: As there is only one specimen in the present collection (Figure 1f) the anatomy is not described. The hinge features (Figure 5a) conform to those figured by Cerulli-Irelli (1908), as do the other shell features. The hinge is very similar to that of *E. clarkiae* Clark (Warén, 1983) (Figure 5c).

Deroux (1961) gave an extensive and comparative description of a shallow-water species commensal with the polychaete *Polydonte maxillosus* Ranzani, 1817, that he identified as "*Lepton subtrigonum* Jeffreys, 1873," and placed in a new genus *Potidoma*. He thought *Potidoma* was congeneric with *Epilepton clarkiae*, not noticing that his new genus would be a synonym of *Epilepton*.

The shell that Deroux (1961) describes has a heavy black or dark brown coating although the shell below is white and translucent. However, the mid-ventral margin of the shell Deroux described is not convex but concave and the position of the umbo and antero-dorsal shell margin differs considerably from the true *E. subtrigonum* and to previous accounts about it (Jeffreys, 1875; Cerulli-Irelli, 1908) (Figure 1f). The hinge also differs in its structure (Figure 5b) and, perhaps of less importance, is the much smaller size of the original and present specimens of *E. subtrigonum* as compared with those described by Deroux (1961). It should also be pointed out that there is a very great difference in their depths of occurrence. The species described by Deroux may well be an *Epilepton*, it is doubtful whether it is identical to the *E. subtrigonum* that Fischer (1873) described.

Epilepton elpis n.sp.

Figs 1e, 2, 3, 4 & 6

Type locality: North America Basin, 35°50.0'N 64°57.5'W, 4833 m

Type specimen: Holotype and paratype, Natural History Museum, London

Material: Atlantis II 24, station 121, 35°50.0'N 65°11.0'W, 4800 m., 1; station 122, 35°50.0'N 64°57.5'W, 4833 m., 5 spec.

Distribution: Abyssal depths in the North America Basin.

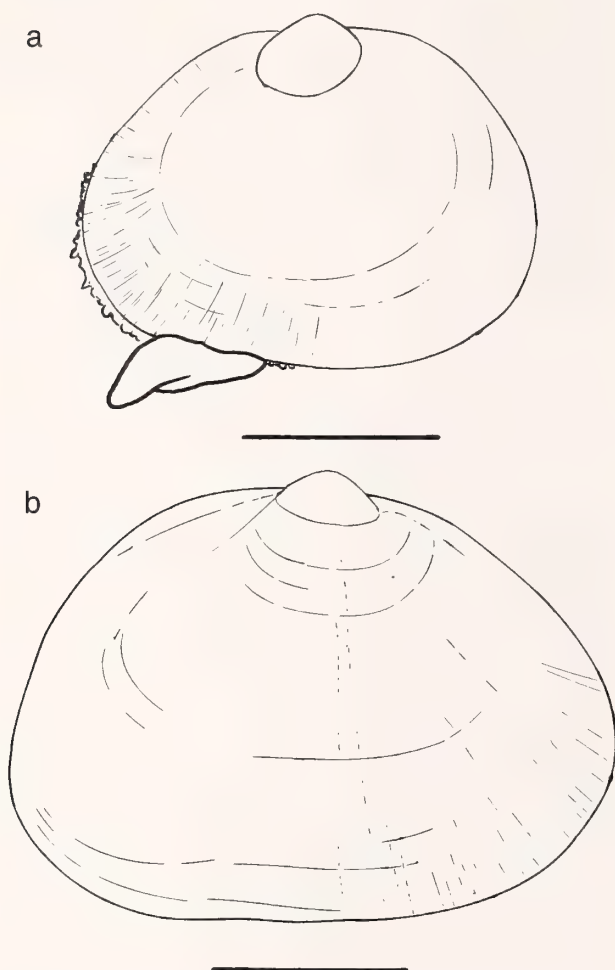


Figure 2. *Epilepton elpis* a) lateral view of shell (Station 122) from left side showing protruding foot and sensory papillae of anterior pedal margin; b) lateral view of shell (Station 121) from right side. Scale bars = 1 mm.

Shell description: Small (<6.5 mm in length), somewhat triangular (sub-trapezoidal) with maximum shell length markedly ventral to mid-horizontal line, elongate (length/height ratio: 1/0.75), slender (length/width ratio: 1/0.29), extremely fragile, white, in some specimens faint anterior marginal radial ridges correspond to region of sensory mantle tentacles, few faint growth lines present; umbo moderately prominent, slightly anterior to the mid-vertical line; shell margin highly characteristic, postero-dorsal margin relatively straight for short distance before broadly curving to the posterior limit of shell, antero-dorsal margin slopes steeply and relatively straight to approximately the mid-horizontal line before curving to anterior limit of shell and continuing to ventral margin; ventral margin in most specimens shallowly curved, in others almost straight or even slightly concave posterior to mid-

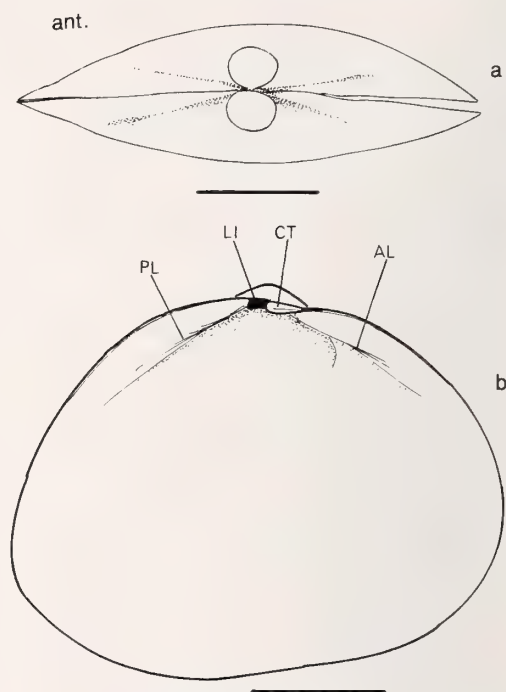


Figure 3. *Epilepton elpis* a, internal view of a left valve (station 121) to show detail of hinge; dorsal view of shell (station 121). Scale bars 1 mm. AL anterior lateral tooth, CT cardinal tooth, LI ligament, PL posterior lateral tooth.

vertical line; hinge-plate elongate, posteriorly broad, less so anteriorly, anterior and posterior lateral teeth at ventral margin of the hinge-plate slender, single posteriorly oblique cardinal tooth in each valve, meets shell margin immediately posterior to beak; internal ligament short and opisthodontic, lies close to margin of hinge-plate posterior to cardinal tooth, internal and external layers clearly marked, posterior external ligament of fused periostracum short, very small anterior external ligament present; prodissoconch extremely large, 1.04 mm total length.

Internal morphology: Anterior sensory fold of mantle margin of pedal aperture finely papillate (28 papillae on each mantle edge in a specimen 4 mm. total length), a moderately broad band of mantle glands lie immediately internal to inner muscular fold of pedal aperture and dorsally delineated by an irregular epithelial ridge, sensory folds posterior to the pedal gape with eight papillae, simple posterior exhalant and 'inhalant' apertures the former formed by mantle fusion the latter by adhesion of the opposing inner mantle folds; anterior and posterior adductor muscles circular in cross section, posterior adductor slightly larger than anterior; foot relatively large and broad; posterior and anterior retractor muscles well-developed; pedal glands present with 5-6 byssal threads; gills

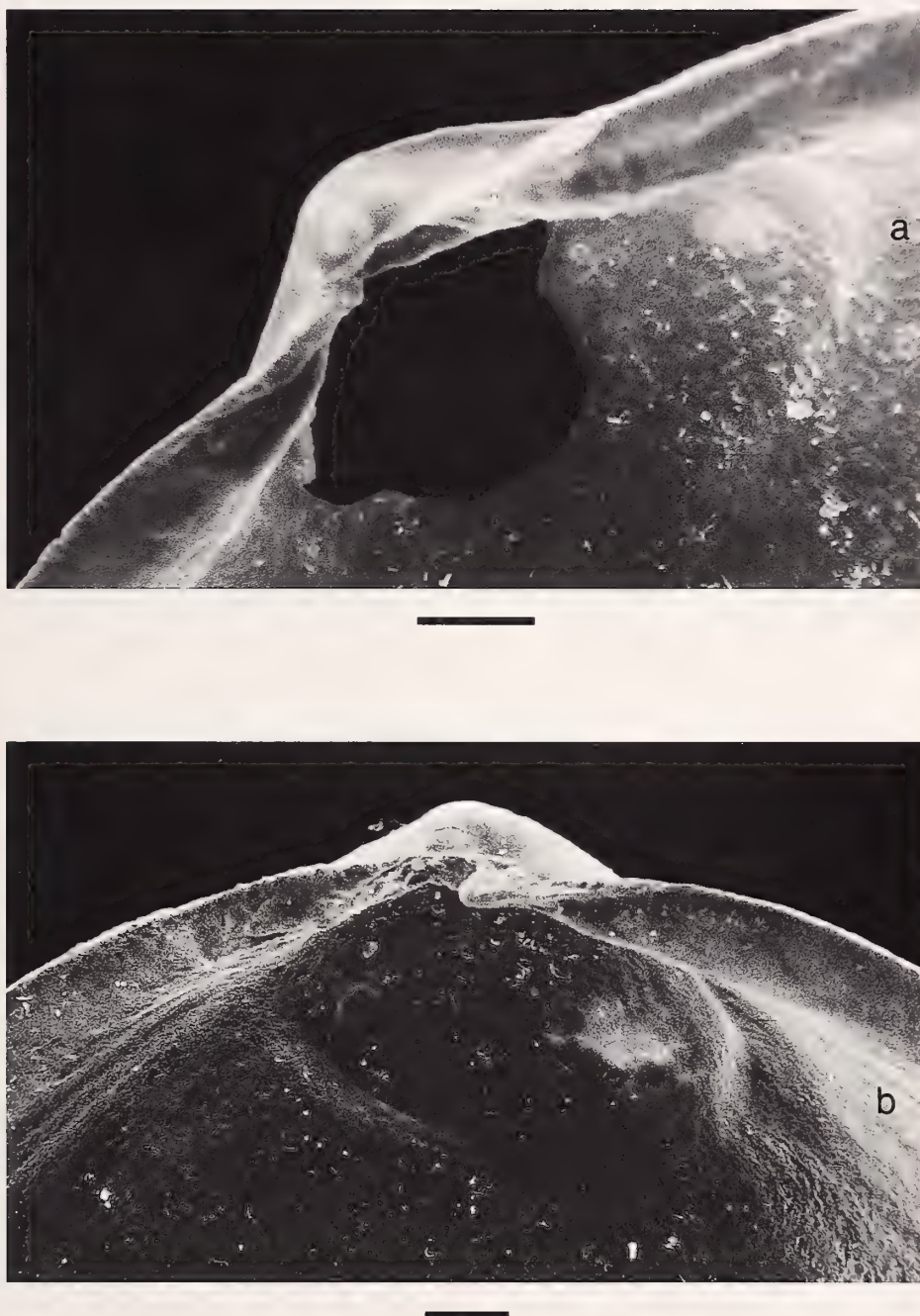


Figure 4. *Epilepton elpis* a and b) Internal views of the hinge of the right and left valves (station 122) to show detail of the hinge. Scale bars = 0.1 mm.

homorhabdic, not plicate, outer demibranch absent, inner demibranch with ascending and descending lamellae composed of approximately 35 filaments, ventral groove of demibranch not marked, axes of ascending lamellae fused to body wall and to each other

posterior to foot; palps small with approximately 8 internal ridges; mouth opens to relatively elongate oesophagus, stomach elongate with midgut and style sac combined, hindgut extends anteriorly for a short distance before turning posteriorly along the dorsal

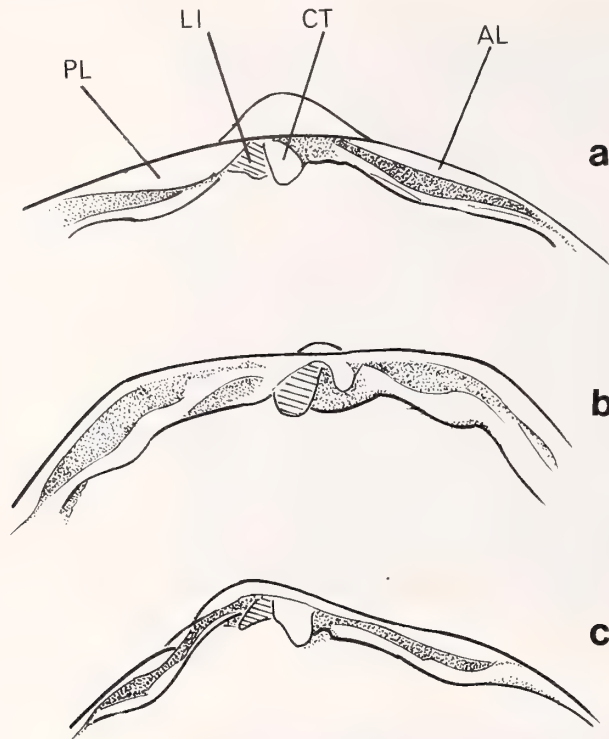


Figure 5. Species of *Epilepton*. Semidiagrammatic illustrations of the left hinges of a, *E. subtrigonum*; b, "*Potidoma subtrigonum*" (after Deroux, 1961); c, *E. clarkiae* (after Tebble, 1966). AL anterior lateral tooth, CT cardinal tooth, LI ligament, PL posterior lateral tooth.

margin to pass over posterior adductor to anus; visceral, cerebral and pedal ganglia small, with very fine connectives: gonad immature in stained specimen.

Remarks: This species is named after Elpis (Hope) the only item left in Pandora's box after she had opened it. It is a truly abyssal species. It differs from *E. clarkiae*, *E. Parrussetensis*, *E. solidulum* and *E. subtrigonum*, in shell proportions (Figure 1), in differences in the position of the umbo in relation to the length of the shell, the less curved ventral margin, the less prominent lateral teeth and the more oblique ligament and relatively weak cardinal tooth.

DISCUSSION

In addition to the five species listed above, a further three Atlantic species may belong to the genus. One, described under the name *Mancikellia divae* by Aartsen and Carrozza (1997), is considered to be a species of *Epilepton* by Giribet & Peñas (1998). A second, already discussed (p. 2), is that described by Deroux (1961) as "*Potidoma subtrigonum*." A possible third discovered when searching relevant literature was described and named by Dall (1899) as *Erycina? fernandina*. As recognised by Abbott (1974), this does not belong to

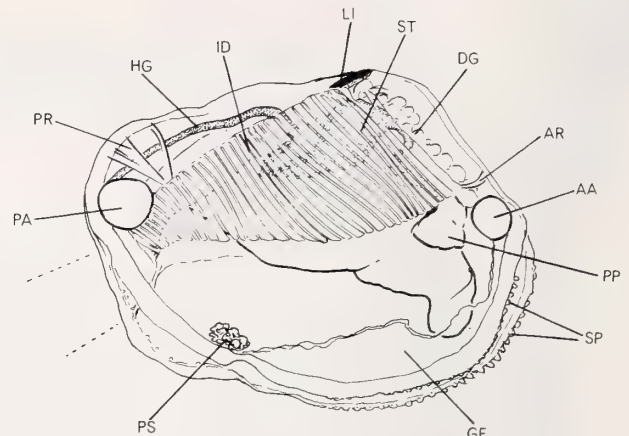


Figure 6. *Epilepton elpis* Semidiagrammatic view of the internal anatomy of a specimen from Station 122 as seen from the right side. AA anterior adductor, AR anterior pedal retractor, DG digestive gland, FT foot, GE glandular epithelium, HG hindgut, ID inner demibranch, LI ligament, PA posterior adductor, PP palp, PR posterior pedal retractor, PS pseudofaeces, SP sensory mantle papillae, ST stomach. Scale bar = 1 mm.

the genus *Erycina* but may, on further examination, prove to be an *Epilepton*.

Bivalves of the order Galeommatoidea are notoriously difficult to identify and there has been considerable debate as to their relationships with other orders. Salas & Gofas (1998), in particular, have suggested that *Neolepton* is a paedomorphic veneroidean. Certainly the hinge characters of *Neolepton* suggest this could be so (Allen, 2000). In contrast, the hinge of *Epilepton* differs considerably from that of *Neolepton* and the veneroideans. Although, like *Neolepton*, *Epilepton* has elongate posterior and anterior lateral hinge teeth instead of a complex series of cardinal teeth, *Epilepton* has a single cardinal that may or may not be particularly strong. There is a strong case for removing *Epilepton* from the Neoleptonidae. A transfer to the Montacutidae was suggested by Deroux (1961), debated by Bowden & Heppell (1968), and concurred by Salas & Gofas (1998). Unlike *Neolepton*, *Epilepton* has no exhalant siphon. Furthermore, *Epilepton* has sensory papillae at the mantle edge of the pedal aperture (Figure 7), a feature not present in *Neolepton*.

The new species described here differs in one respect from described species of the family Montacutidae. In the two specimens in which the soft parts were examined an 'inhalant' aperture was defined by a short adhesion of the opposite inner muscular folds of the mantle. Apart from this the mantle margin is similar to other species of the family Montacutidae, i.e., a papillate sensory fold with the papillae particularly numerous anteriorly, and an exhalant aperture that is not

siphonate. It is likely that in *E. elpis* water flow into the mantle cavity is via the anterior papillate area of the mantle gape and that the posterior 'inhalent' aperture is the point at which the pseudofaeces are voided.

Epilepton clarkiae and *E. parrussetensis* are more ovate and anteriorly extended than the other species listed here. Nevertheless, the hinge structure is similar (Figure 5), and where described, so too is the internal anatomy. At present, there is no reason for them to be separate genera. The sub-trapezoidal shape and the shallowly curved ventral shell margin, which in the case of *E. elpis* maybe slightly concave mid-ventrally, is reminiscent of the genus *Pseudopythina* and may indicate similarity in habit. Species of *Pseudopythina* are commensals that are typically byssally attached to other species [e.g., *P. rugifera* (Carpenter, 1864) attached to *Upogebia pugettensis* (Dana, 1852), Narchi (1963)]. In fact, *Epilepton clarkiae*, although not of this shape, has recently been proved to be commensal with *Phascolion stromi* (Delongueville & Scaillet, 1999). However, the hinge of *Pseudopythina* is without anterior and posterior lateral teeth, and it must be assumed that the similarity in shape with *E. elpis* may be related to the epibyssate habit of the two genera.

Apart from the reduction of the ctenidia to single inner demibranchs as seen in *E. elpis*, there is little deviation from the typical eulamellibranch anatomy. Reduction of the ctenidia is almost universal in deep-sea bivalves, particularly those of a small size. This may simply be related to small size, although respiratory demands probably differ at great depths due the effect of pressure on physiological processes.

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Effects of Photoperiod Manipulation on Reproductive Condition of the Northern Bay Scallop, *Argopecten irradians irradians* (Lamarck, 1819)

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Abstract. Recent studies suggest that photoperiod may play an important role in reproductive development of certain scallop species, but similar investigations have not been done previously for the bay scallop. In this study, we exposed bay scallops, *Argopecten irradians irradians* (Lamarck, 1819), during late reproductive development but prior to spawning, to three different light regimens (24 hr light, 24 hr dark, and ambient light) in the laboratory. Scallops from all treatments showed increases in reproductive condition over a 4-week period, but those held under continuous light showed a statistically greater increase in reproductive condition as early as 6 days after the start of the experiment. Our data suggest that photoperiod may play a significant role in affecting the reproductive condition of bay scallops.

INTRODUCTION

Changes in water temperature and food availability are generally regarded to be the major exogenous factors that cue the process of reproductive development in temperate bivalve mollusks (Sastry, 1963, 1966, 1968; Sastry & Blake, 1971; Bayne, 1976; Newell et al., 1982; MacDonald & Thompson, 1985). Photoperiod has usually been viewed as playing a minor role, or no role whatsoever, in gametogenesis of bivalves, but given the well-developed nature of the pectinid eye, it is probable that light plays an important role in scallop reproduction (Devauchelle & Mingant, 1991). Evidence is mounting that photoperiod may be important in the reproductive development of such pectinid species as *Pecten maximus* (Paulet & Boucher, 1991; Devauchelle & Mingant, 1991; Saout et al., 1999), *Placopecten magellanicus* (Couturier & Aiken, 1989), and *Argopecten circularis* (Villalejo-Fuerte & Ochoa-Baez, 1993). While reproduction has been extensively studied in the bay scallop, *Argopecten irradians* (see review by Barber & Blake, 1991); effects of photoperiod on gonadal maturation have not been investigated. The purpose of this study was to examine how manipulation of photoperiod affected gonad weight and reproductive (gonadal) index during the late stages of reproductive development, prior to spawning, of the northern bay scallop, *Argopecten irradians irradians*.

MATERIALS AND METHODS

Effects of photoperiod manipulation on bay scallop reproductive development were monitored over a 4-

week period, from mid-May to mid-June 2003, by exposing 0+ yr hatchery-reared scallops which had been overwintered in Goose Creek, Southold, New York, USA to three different light regimens: (1) ambient light (diurnal sunlight approaching maximum day-length in late June), (2) continuous darkness (effected with light impermeable fiberglass tanks and covers), and (3) continuous light (provided by an overhead bank of four 1.23 m long, 40-watt Cool White® fluorescent light tubes). Each of the three groups of scallops (n = 95) was held in separate opaque, fiberglass raceway tanks (0.9 m wide × 2.5 m long × 0.6 m deep) supplied with unfiltered, ambient flowing seawater from Cedar Creek at the Southold Marine Environmental Learning Center in Southold, New York. Flow rate was 113.61 (=30 gal)/min; temperature ranged from 14.4–18.9°C, while salinity remained at ~28 ppt during the study period. All tanks were cleaned on a weekly basis, following removal of scallops, with a strong stream of water. At the time of initial collection on 14 May 2003, shell heights of 15 scallops were measured to the nearest mm (\bar{x} = 48 mm; SD = 3.3 mm) and a baseline of reproductive condition of these animals was determined via measurement of gonad dry weight (GDW) and gonadal index (GI = (gonad dry weight) / (total tissue dry weight) × 100) (Barber & Blake, 1991). Shell heights, GDW, and GI of 15 bay scallops sacrificed from each of the three photoperiod treatments (ambient, dark, light) were similarly measured at approximately weekly intervals during the ensuing 4-week period.

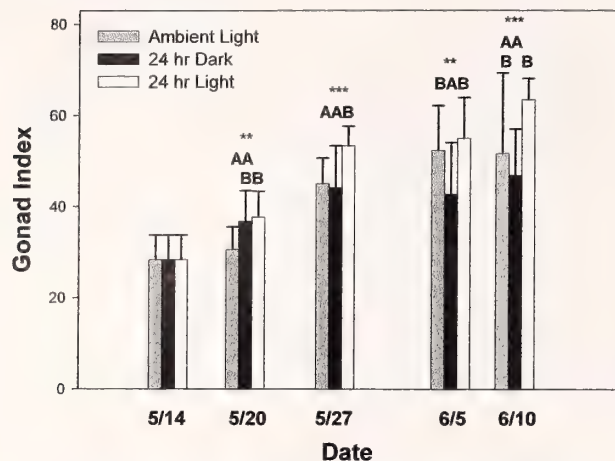


Figure 1. Temporal changes in gonad index (GI) of hatchery-reared 0+ yr bay scallops, *Argopecten irradians irradians*, exposed to three different light regimens (ambient light, 24 hr dark, 24 hr light) in the laboratory from 14 May–10 June 2003. Bars represent mean values \pm 1 SD; $n = 15$ individuals per group, per sample date. Statistical differences between means for a given date, as determined via Kruskal-Wallis non-parametric ANOVA, are shown above the bars; ** = $P < 0.01$; *** = $P < 0.001$. Letters shown above the bars signify results of Tukey-type non-parametric multiple comparisons; dates having the same letter are not statistically different at $P < 0.05$.

RESULTS

Bay scallops held under each of the three different photoperiod treatments (ambient, 24 hr dark, 24 hr light) showed progressive increases in reproductive condition, as evidenced by increases in mean GI and mean GDW by the end of the 4-week study period (Figures 1, 2). Scallops held under the 24-hr light regimen showed a consistent increase in both GI and GDW at each of the four sampling periods, while scallops held under ambient photoperiod or continuous darkness showed an increase in GI and GDW for the first 2 weeks, but some fluctuation thereafter. There was no evidence that extensive spawning occurred in any of the scallop groups, as would have been evidenced by a sharp decline in GI and GDW following a steady increase (Barber & Blake, 1991).

Significant differences in reproductive condition of scallops from the three groups were apparent as early as 6 days after exposing scallops to the different photoperiods (Figures 1, 2). Raw and transformed GI and GDW values were non-normal, so parametric analyses were precluded, but Kruskal-Wallis non-parametric ANOVA's (Zar, 1984) of GI versus photoperiod treatment, at each of the four sampling dates, were each statistically significant at $P < 0.01$ (Figure 1). Following these analyses, Tukey-type non-parametric multiple comparisons (Zar, 1984) showed

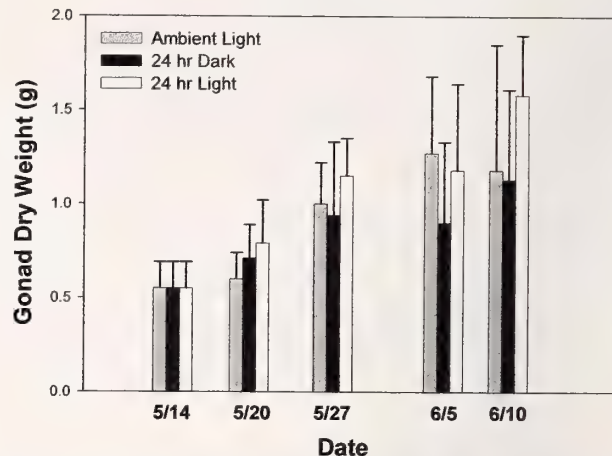


Figure 2. Temporal changes in gonad dry weight (GDW) of hatchery-reared 0+ yr bay scallops, *Argopecten irradians irradians*, exposed to three different light regimens (ambient light, 24 hr dark, 24 hr light) in the laboratory from 14 May–10 June 2003. Bars represent mean values \pm 1 SD; $n = 15$ individuals per group, per sample date. While there were statistical differences (at $P < 0.04$) between means on 5/20, 6/5, and 6/10, as determined via Kruskal-Wallis non-parametric ANOVA's, there were no statistical differences (at $P < 0.05$) shown in any of the Tukey-type non-parametric multiple comparisons.

that GI of scallops held under 24-hr light was significantly higher, at $P < 0.01$, than GI of ambient scallops on 20 May, significantly higher than GI of both ambient and 'dark' scallops on 27 May, and significantly higher than those of 'dark' scallops on both 5 June and 10 June. Comparable Kruskal-Wallis ANOVA's of GDW versus photoperiod treatment were significantly different, at $P < 0.04$, for the 20 May, 5 June, and 10 June sample dates, but were not different on 27 May ($P = .0651$). Tukey-type multiple comparisons, however, did not reveal significant differences, at $P < 0.05$, between GDW of scallops from the three treatment groups on any of the four sampling dates. No differences in shell heights of scallops were apparent during the course of the study, as revealed by a 2-way parametric ANOVA of shell height versus photoperiod treatment ($P = 0.0911$), sample date ($P = 0.1267$), and treatment \times date interaction ($P = 0.234$). No scallop mortality was recorded during the study.

DISCUSSION

Our data suggest that photoperiod may play a significant role in affecting the reproductive condition of bay scallops, *Argopecten irradians irradians*. Effects of photoperiod manipulation were also manifested rapidly, as early as 6 days after deployment of scallops under the three different photoperiod regimens. Bay scallops exposed to the different photoperiods all showed

increases in reproductive condition (both GI and GDW) over the course of the 4-week study, but, relative to initial values, scallops exposed to 24-hr light had significantly higher GI levels than those of scallops exposed to ambient light or 24 hr dark conditions. The lack of clear statistical differences amongst GDW of scallops in the three photoperiod treatment groups was likely due to variability of gonad weights of scallops used in the experiment.

Photoperiod was the only variable manipulated in our experiments, and thus we conclude that the manipulation of photoperiod was directly responsible for the observed differences in scallop reproductive development. A potential indirect effect of light manipulation might have been an elevated level of algal growth, and hence food, in experimental tanks exposed to longer photoperiods. Walls of the 24 hr-light tanks qualitatively appeared to have a heavier biofilm layer than those of the other tanks at the time of the weekly cleanings. Given the flow rate in the tanks (113.61 (=30 gal)/min), however, it is unlikely this could have affected seston levels in the tanks. While benthic microalgae may be potentially important to the diet of bay scallops (Davis & Marshall, 1963), it does not seem likely that this nutritional source would have been significantly different in the three tanks due to the frequency with which tanks were cleaned. Thompson et al. (1994) showed that larvae of *Patinopecten yessoensis* (= *P. caurinus yessoensis*) grew faster and were larger after 18 d when fed phytoplankton (*Pavlova lutheri* or *Chaetoceros simplex*) grown under high vs. low light levels; they concluded that this difference was due to the higher levels of short-chain saturated fatty acids in the algae grown under high light conditions. Again, given the high flow rate and very brief residence time of phytoplankton in our tanks, it is unlikely that the different light regimens affected the biochemical composition of the ambient phytoplankton species while in the tanks.

Our conclusions about the effects of photoperiod on reproductive development in *Argopecten irradians* appear to corroborate the conclusions of Devauchelle & Mingant (1991). These authors demonstrated that *Pecten maximus* showed accelerated gametogenesis when exposed to increased photoperiod length (15 hrs light increased to 15.15 or 18.3 hrs light), compared to scallops held under short and constant light (8 hr) or when photoperiod length was reduced (from 14 or 15 hrs light to 8.3 hrs). Furthermore, they found that decreasing photoperiod reduced gametogenic activity and numbers of eggs spawned by mature *Pecten maximus*.

The effects of photoperiod manipulation may be of value to scallop aquaculture. Exposure of scallops to longer photoperiods might potentially result in faster, or in higher levels of, egg production, as determined by

Devauchelle & Mingant (1991). In our study, the mean GI values for scallops exposed to continuous light for between 2–4 weeks (53.3–63.4) were considerably higher than maximum mean GI values reported for 0+ yr scallops from natural populations (Epp et al., 1988: 29.2–32.0; Tettelbach et al., 1999: 33.1–38.0; Tettelbach et al., 2002: 37.0–44.5) and hatchery stocks (Davidson, 2000: 30.1–34.1; Tettelbach et al., 2002: 35.2–35.8) sampled from the field in eastern Long Island, New York at comparable times in the reproductive cycle, mid-May to mid-June. While the high GI levels that we observed may be reflective of differences in relative reproductive investment of scallops from different source populations (Parsons et al., 1992), they also appear to reflect the positive effects of exposure to longer photoperiod. Further investigation of the effects of light on the reproductive development of bay scallops should provide further scientific insight as well as potentially useful applications to aquaculture.

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Cenozoic Atlanto-Mediterranean biogeography of *Spiricella* (Gastropoda, Umbraculidae) and climate change: Filling the geological gap

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Abstract. *Spiricella unguiculus* Rang & Des Moulins, 1828 is a thermophilic opisthobranch species, occurring today in the eastern Atlantic from southern Portugal to Mauritania, and the Mediterranean. However, during its geological history, the species had a much broader geographic distribution, including also the North Sea basin and more northern Atlantic coasts of Western Europe.

For more than 150 yr the species was known from a single specimen from the Atlantic Lower Miocene of the Aquitaine basin, France. More recently the species has been recorded from the European Oligocene, Miocene and Recent faunas. The discovery of *Spiricella unguiculus* in the Pliocene of the Mondego Basin (central-west Portugal) fills the gap existing in the geological distribution of the species. Although the overall recorded occurrences of the species are rare, the Cenozoic geographical distribution of *S. unguiculus* appears to have undergone a sharp southward contraction. This contraction is in accordance with the general biogeographic trend observed for other Atlanto-Mediterranean gastropod taxa and with the Neogene to Recent Northern Atlantic cooling scenario.

Key Words: Gastropoda, Opisthobranchia, Umbraculidae, *Spiricella unguiculus*, Pliocene, Atlantic, Portugal, Palaeobiogeography.

INTRODUCTION

Opisthobranch mollusks have reduced thin-walled shells or no shell at all. Consequently, these mollusks have a low fossilization potential and a relatively poor fossil record, when compared with most groups of gastropods. Therefore, as stressed by Valdés & Lozouet (2000), with the exception of the Cephalaspidea and the pteropods, little is known about fossil Opisthobranch molluscs.

Spiricella Rang & Des Moulins, 1828, a monospecific opisthobranch gastropod genus, is a good example of this. *Spiricella unguiculus* Rang & Des Moulins, 1828, an Atlanto-Mediterranean thermophilic species, has a remarkably long geological history, spanning from the Oligocene to Recent, yet probably more papers have been written on this enticing little gastropod than there are specimens, fossil or Recent.

Until twenty years ago the species was known only from one specimen from the Lower Miocene of Aquitaine. Since then, a series of papers have increased its geochronological range dramatically, making it one of the most long lived Cenozoic gastropod species known and, more important, an excellent biogeography case study. *Spiricella unguiculus* has been reported from the Lower Oligocene, Rupelian stage, of the Aquitaine basin, south-western France (Valdés & Lozouet, 2000), from the Lower Miocene, Aquitanian and Burdigalian stages, of the Aquitaine basin (Rang & Des Moulins, 1828; Peyrot, 1932; Dekker, 1987; Valdés & Lozouet, 2000; Lozouet, Lesport & Renard, 2001); from the Middle Miocene, Hemmoorian stage, Aalten Member, Netherlands (Janssen, 1984) and from the Pliocene, uppermost Zanclean to lower Piacenzian stages, of the Mondego basin, central-West Portugal (this paper).

At the same time, the species has seen its geographical occurrences expanded from south-western France (Oligocene-Miocene: Rang & Des Moulins, 1828; Valdés & Lozouet, 2000) to the North Sea basin (Miocene: Janssen, 1984), and Western Iberia (Pliocene: this paper). *Spiricella*

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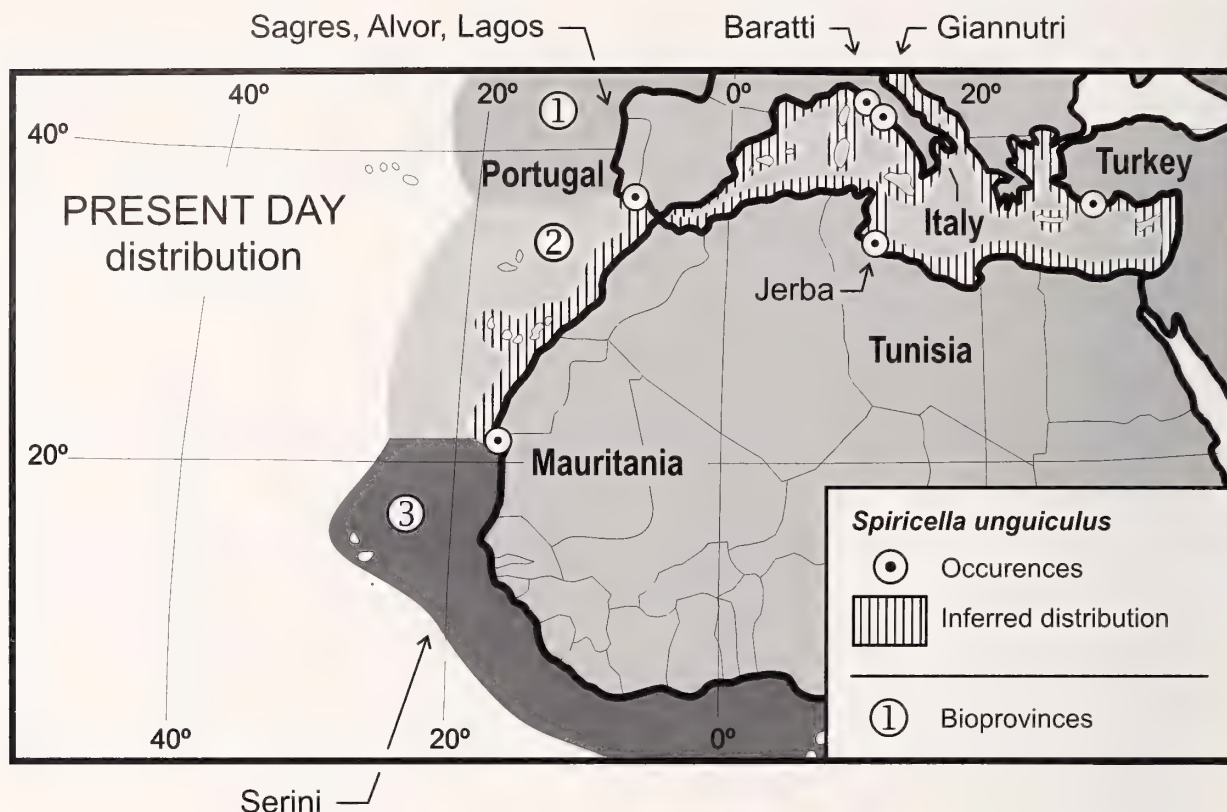


Figure 1. Present day geographic distribution of *Spiricella unguiculus* and molluscan biogeographic provinces (after Raffi, Stanley & Marasti, 1985). 1 - French-Iberian province; 2 - Mediterranean-Moroccan province; 3 - Mauritanian-Senegalese province.

unguiculus is essentially subtropical in distribution. In the present day, it occurs in the Eastern Atlantic, in the southern coast of Portugal (between Alvor and Lagos: Hoeksema & Janssen, 1984; Geuze & Hoeksema, 1994) and in Mauritania, West Africa (Serini: Geuze & Hoeksema, 1994), and in the Mediterranean, in Italy (bay of Baratti, south of Livorno: Carozza & Rocchini, 1987; island of Giannutri: Angioy & Nikolay, 1993), in Tunisia (island of Djerba: Carozza & Rocchini, 1987) and in Turkey (locality unknown; see Valdés & Lozouet, 2000) (Figure 1).

Although described from several Oligocene to Pliocene localities, and reported from the present day Atlanto-Mediterranean region, the species always seems to be uncommon, known from less than a dozen fossil and Recent shells. What is more, nothing is known of the animal.

Until now, there was a gap in the geological history of the genus. *Spiricella* was unknown from Upper Neogene formations. Recent work on the Atlantic Pliocene of the Mondego basin, at the Vale de Freixo outcrop, central-west Portugal, has yielded one specimen of *S. unguiculus*. This exciting find, reported herein, fills the existing gap in the genus geological history, making it possible to trace its entire bio-

geographical evolution and, more important, to correlate it to late Cenozoic Atlanto-Mediterranean molluscan biogeography and global climatic change.

GEOLOGICAL SETTING

Vale de Freixo is located in central-west Portugal (Pombal region) in the Mondego Cenozoic basin (Figure 2). The fossiliferous beds of this locality are Pliocene, uppermost Zanclean to lower Piacenzian, in age (Cachão, 1990; Silva, 2001). The calcareous nannofossil assemblage from these beds indicates placement in the biozone CN12a of Okada & Bukry (1980), after Cachão (1990).

The Atlantic marine malacofauna of Vale de Freixo, as well as all the marine Pliocene molluscan assemblages of the Mondego basin, correlate to the Pliocene MPMU1 (Mediterranean Pliocene Molluscan Unit 1) as defined by Monegatti & Raffi (2001) for the Mediterranean (Silva, 2001).

During the very end of the Zanclean and the beginning of the Piacenzian the Caldas da Rainha - Marinha Grande - Pombal region corresponded, generally speaking, to a shallow sea of warm waters, significantly warmer than today at that latitude, and

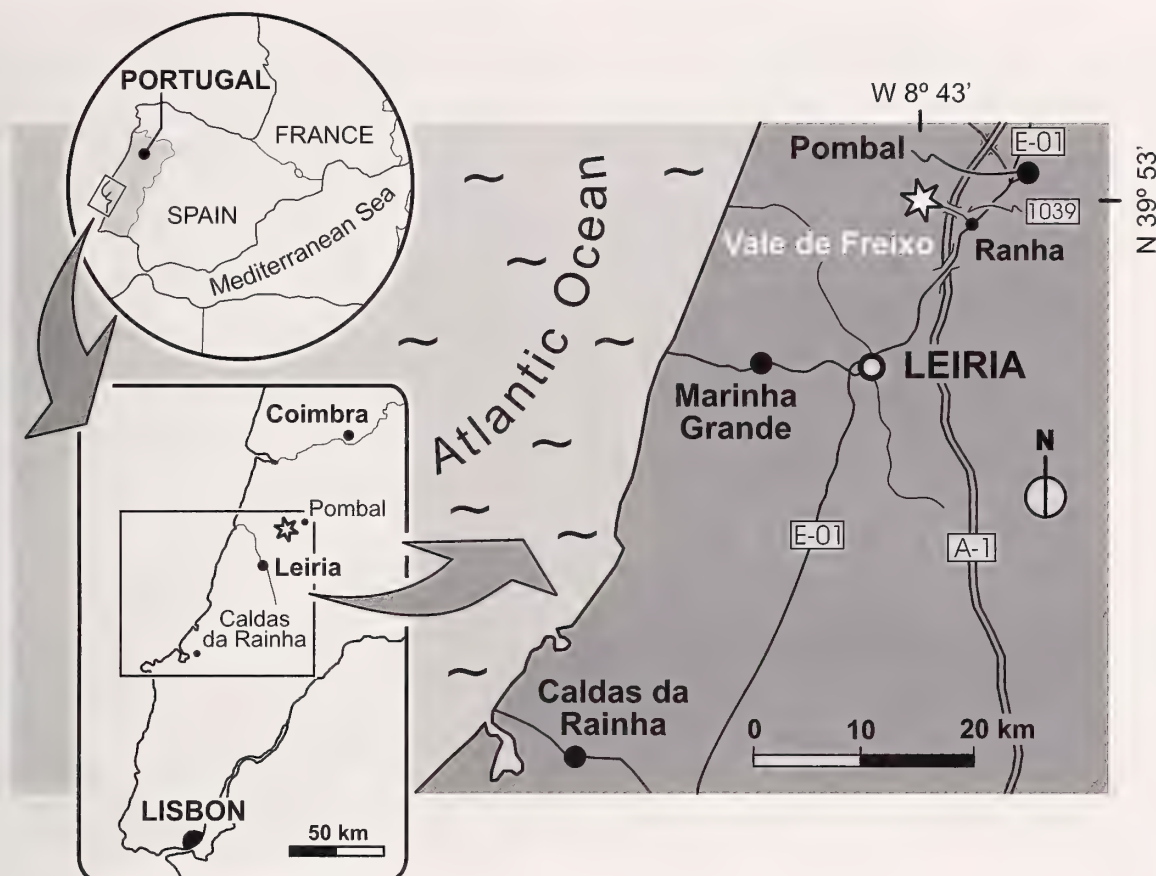


Figure 2. Geographic location of the Vale de Freixo outcrop. Central-West Portugal.

normal marine salinity, somehow protected from the direct influence of the open Atlantic ocean (Nolf & Silva, 1997; Silva et al., 2000; Silva, 2001).

For further details, general stratigraphical setting of the Mondego basin, graphic columnar section of Vale de Freixo, and additional palaeomalacological references see Gili et al. (1995), Silva et al. (2000), Dell'Angelo & Silva (2003).

SYSTEMATIC PALAEONTOLOGY

Subclass Opisthobranchia Milne-Edwards, 1848

Order Notaspidea P. Fischer, 1883

Superfamily Umbraculoidea Dall, 1889

Family Umbraculidae Dall, 1889

Genus *Spiricella* Rang & Des Moulins, 1828

Spiricella unguiculus Rang & Des Moulins, 1828

Figure 3

1928 *Spiricella unguiculus* Rang, 1828 - Rang & Des Moulins, p. 227, pl. 1, figs. 1–5.

1932 *Spiricella unguiculus* Rang, 1827 - Peyrot, p. 297, pl. 18, figs. 38–39, 42 (holotype).

1984 *Spiricella unguiculus* Rang, 1827 - Janssen, p. 386, pl. 19, fig. 19a–d.

1984 *Spiricella unguiculus* Rang, 1827 - Hoeksema & Janssen, p. 7, figs. 1–8.

1987 *Spiricella unguiculus* Rang, 1827 - Carozza & Rocchini, p. 63, fig. 1a–c.

1987 *Spiricella unguiculus* Rang, 1827 - Dekker, p. 225, fig. 1.

1994 *Spiricella unguiculus* Rang, 1827 - Geuze & Hoeksema, p. 225, fig. 1–3.

2000 *Spiricella unguiculus* Rang and Des Moulins, 1828 - Valdés & Lozouet, p. 459, pl. 2, figs. 7–10.

2001 *Spiricella unguiculus* Rang, 1828 - Lozouet, Lesport & Renard, p. 84, figs. 19d–e.

2001 *Spiricella unguiculus* Rang, 1827 - Silva, p. 590, fig. 3.201.

Material: One specimen (N° VFX.03.381, Carlos Marques da Silva coll., Geology Department, Sciences Faculty of the University of Lisbon), relatively well-preserved, from bed 3 of the Vale de Freixo outcrop, Pombal region, central-west Portugal. Pliocene, uppermost Zanclean to lower Piacenzian; calcareous nannofossils biozone CN12a of Okada & Bukry (1980); Mediterranean Pliocene Molluscan Unit 1 of Monegatti & Raffi (2001).

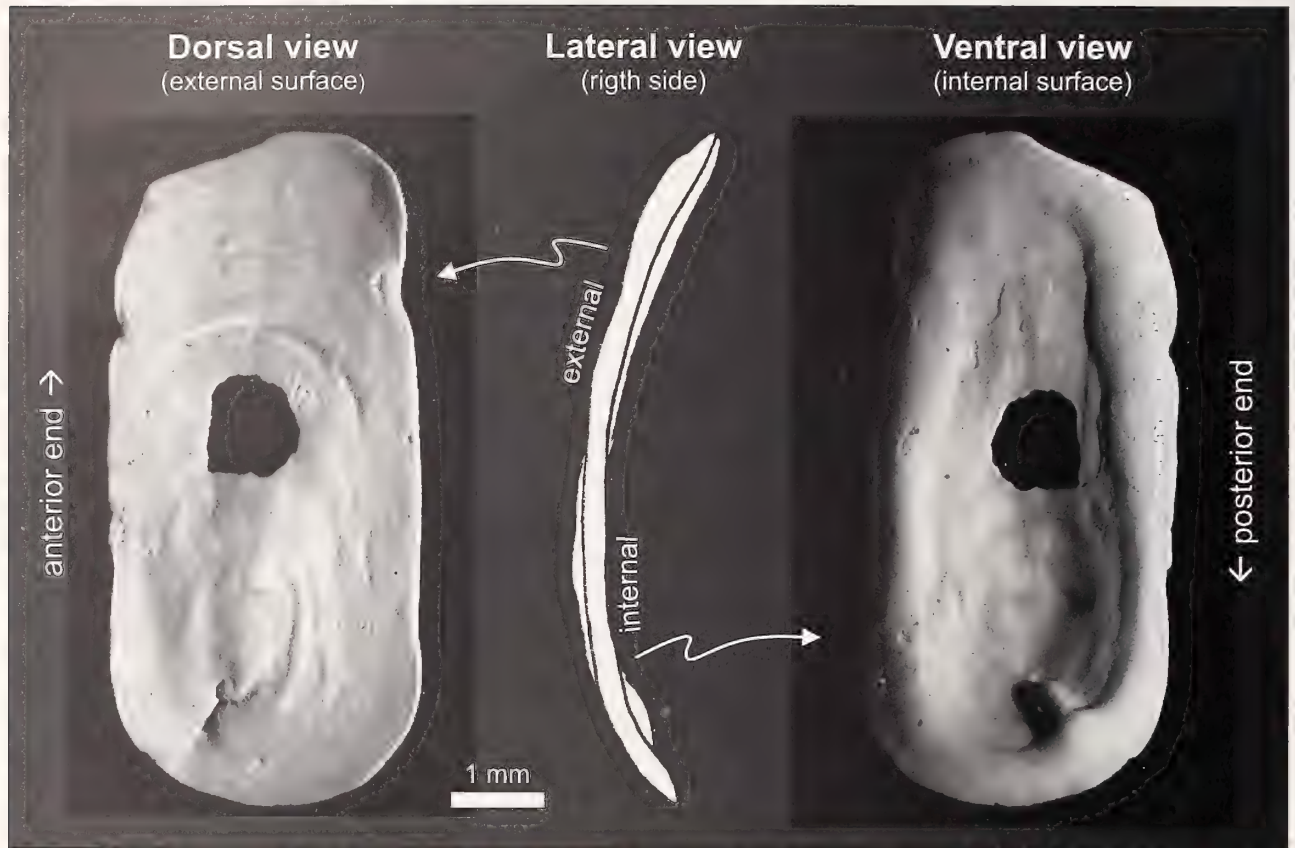


Figure 3. *Spiricella unguiculus* Rang & Des Moulins, 1828. Specimen VFX.03.381. Length: 7.3 mm. Vale de Freixo, Mondego Basin, Portugal. Pliocene.

Description: Shell small, 7.3 mm long, 3.4 mm width, thin, fragile, unguiform, subrectangular, antero-posteriorly elongate, with parallel sides and rounded extremities, convex profile on the dorsal side. Apex eccentric, placed approximately one sixth of the total length from the posterior edge and slightly to the left. A narrow rectilinear sulcus runs obliquely from the apex to the edge of the posterior border. Protoconch paucispiral, naticiform, sinistrally coiled, arranged in the horizontal plane, consisting of 1.5 smooth whorls, diameter 333 μm , with a medium-sized nucleus, diameter 88 μm . The protoconch is partially embedded within the surface of the shell. Transition to teleoconch sharply delimited. Sculpture of the teleoconch absent, except for concentric growth lines, more strongly developed on the anterior part of the dorsum, giving it a rugose appearance. The growth lines are much finer and sometimes subobsolete on the anterior part. Edge sharp. Ventrums smooth and shiny, with a rounded, thickened rim of variable width (about $\frac{1}{4}$ the shell width: 0.6–0.8 mm). A tenuous horseshoe-shaped continuous muscle scar is present on the posterior part on the inner edge of the rim, with the open end facing

forward. The apex and sulcus are represented on the inner aspect by a rounded ridge.

Remarks: Traditionally, the monospecific genus *Spiricella* has been placed in the Umbraculidae (Janssen, 1984; Hoeksema & Janssen, 1984; Carrozza & Rocchini, 1987; Valdés & Lozouet, 2000). Willan (1984) described members of this family as having patelliform shells, with a more or less centrally placed blunt apex and the protoconch arranged in a vertical plane. As previously pointed out by Valdés & Lozouet (2000), the shell shape of *S. unguiculus* is quite different, flattened, elongated, with the apex not prominent and the protoconch arranged in a horizontal plane. This and other differences in the shell ontogeny led Valdés & Lozouet (2000) to consider *Spiricella* to belong to a separate superfamily from Umbraculoidea, but postponed its definitive assignment until soft parts become available to study.

The single Pliocene specimen available from the Portuguese Vale de Freixo outcrop is very similar to those described and figured by other authors (Janssen, 1984; Hoeksema & Janssen, 1984; Carrozza & Roc-

chini, 1987; Valdés & Lozouet, 2000) and agrees with the original description of the species and the holotype (Rang & Des Moulins, 1828; Peyrot, 1932). The protoconch is almost identical in form and dimension to that described and figured by Valdés & Lozouet (2000: pl. 2, fig. 7). Unfortunately, in the Portuguese Pliocene specimen, the protoconch is somewhat worn and, therefore, does not show the distinctive narrow ribbon at its border with the teleoconch described by these authors.

Almost nothing is known of the ecology of this species. In the Pliocene of Vale de Freixo it occurs in fine sandy sediments, in association with a fossil assemblage indicating a subtropical normal salinity marine infralittoral habitat, with a fine sandy substrate (Silva, 2001). The North Sea basin Miocene specimen belongs to an assemblage indicative of an open marine environment of rather shallow water in a subtropical to temperate-subtropical climate (Hoeksema & Janssen, 1984). The Recent Italian specimen was collected from dredgings on a muddy bottom at a depth of about 30 m (Carrozza & Rocchini, 1987) and the specimen from the island of Giannutri, Djerba, Tunisia, at a depth of about 54 m (Angioy & Nicolay, 1993). Both the single specimen collected from the Recent southern Portuguese coast and that found in Serini, Mauritania, were found in fine shell grit taken from a beach also suggesting a shallow marine habitat (Hoeksema & Janssen, 1984; Geuze & Hoeksema, 1994).

BIOGEOGRAPHY OF *SPIRICELLA* AND CLIMATIC CHANGE

Today, the thermophilic gastropod *S. unguiculus* occurs in the Northern Hemisphere on the Eastern Atlantic coast, from Southern Portugal to northernmost Mauritania, and in the Mediterranean (Figure 1). Its distribution basically encompasses the Mediterranean-Moroccan province and the northernmost part of the Mauritano-Senegalese Province (as defined in Raffi, Stanley & Marasti, 1985) or the northernmost part of the northern alternance zone of tropical West Africa (as defined in Le Loeuff and Von Cosel, 1998).

The most northerly records of *Spiricella* are those of the Lower Miocene of the North Sea basin. Janssen (1984) reported the occurrence of the species from the Aalten Member, Miste Bed of Winterswijk-Miste, which is equivalent to the North Sea Hemmorian stage (= Burdigalian, see Kowalewski et al., 2002).

The Early-Middle Miocene was a time of global warming (Zachos et al. 2001; Kowalewski et al., 2002) and in the Eastern Atlantic, according to Brébion (1974), Lozouet & Gourges (1995) and Le Loeuff & Von Cosel (1998) a Euro-West African tropical molluscan province stretched from the West coast of France southwards to Angola. This Euro-West African

province corresponds to the Eastern Atlantic expression of the broader Early Miocene Proto-Mediterranean-Atlantic Region of Harzhauser et al. (2002), which according to the palaeogeography of Rögl (1998), would have roughly included the entire area of the Modern Mediterranean and part of the Eastern Atlantic coast, from the coast of Western France southwards. Earlier, during Oligocene times, again according to Harzhauser et al. (2002), a tropical Mediterranean-Iranian Province, part of the broader Western Tethys Region, covered the area of the modern Mediterranean Sea and probably included the European Atlantic coast up to the Bay of Biscay. Therefore, the presence of the subtropical *Spiricella* in the Oligocene of the Aquitaine basin, approximately on the northern limit of this tropical province is not controversial.

Lower Miocene North Sea basin molluscan assemblages show a strong thermophilic character, well established by the presence of taxa such as Conidae, Ficidae, Olividae, Terebridae, Architectonicidae, and Xenophoridae, amongst others (see, e.g., Sorgenfrei, 1958; Anderson, 1964; Rasmussen, 1968; Janssen, 1984). The low diversity of gastropods such as Conidae, with a maximum of three species, and Terebridae, with a maximum of five species, together with the absence of other typically megathermic gastropod taxa such as *Strombus*, strongly suggests that tropical conditions were not present in the North Sea region during Early to Middle Miocene times. Indeed, during Early-Middle Miocene, the North Sea region was part of a separate northern biogeographical unit from the Euro-West African tropical province: the Boreal province (of Kowalewski et al., 2002) or the Proto-Eastern Atlantic Boreal Region (of Harzhauser et al., 2002), roughly equivalent to the Recent Boreal-Celtic province of Raffi, Stanley & Marasti (1985). According to Hoeksema & Janssen (1984) and Zagwijn & Hager (1987), the southern coast of the Miocene North Sea was characterized by warm temperate or even subtropical climate as indicated, e.g., by the presence of thermophilic molluscs and extensive peats. Again, the presence of *Spiricella* in these deposits agrees with the general thermophilic character of the fossil mollusc assemblages.

Taking the presence of the megathermic gastropod *Strombus* as a proxy of tropical conditions, during the Miocene the northern limit of the Euro-West African tropical province would be located somewhere north of the Aquitaine basin, possibly even farther north than the Loire basin. This assumption is based in the reported presence of several species of *Strombus* in the Aquitaine basin (Peyrot, 1932; Lozouet et al., 2001) and the possible occurrence of a single species of the genus in the Loire basin (Glibert, 1949). Harzhauser et al. (2002) assumed a similar northern extension (up to

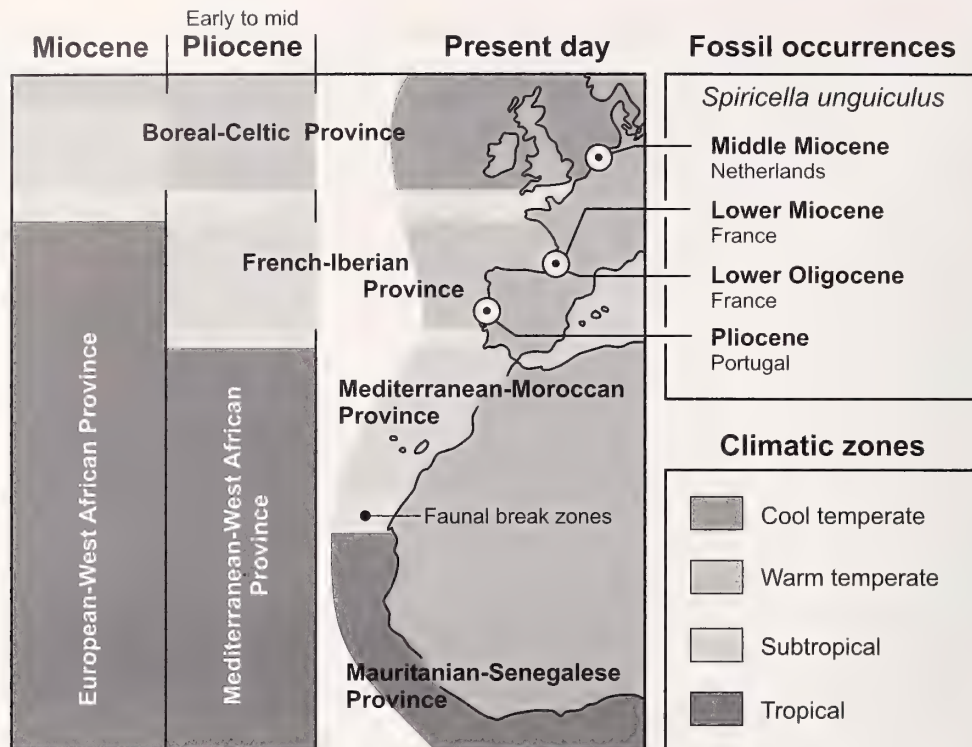


Figure 4. Fossil occurrences of *Spiricella unguiculus* and Neogene molluscan biogeographic provinces of the Atlanto-Mediterranean region. Present day bioprovinces after Raffi, Stanley & Marasti (1985).

the Bay of Biscay) for their Early Miocene Proto-Mediterranean-Atlantic Region.

Hence, since Early-Middle Miocene, north-western France and the Channel region might have represented the southern boundary of the Boreal-Celtic province. Back then, from a climatic point of view, this biogeographic province was characterized by warm temperate to subtropical waters, at least in its southern area, and bordered, to the south-west, with the Miocene Euro-West African tropical province (Figure 4).

In the Pliocene, *Spiricella* is recorded only from the Mondego basin, central-west Portugal. The Pliocene malacofauna of the Mondego basin shows strong thermophilic affinity, again with the presence of taxa such as Conidae and Terebridae, but with poor diversity and lacking *Strombus* (Silva, 2001). Once more the presence of *Spiricella* in these deposits agrees with the subtropical character of the fauna.

Cenozoic climate in the Atlanto-Mediterranean region, and indeed in the Northern Hemisphere, is marked by a relatively steady long term Oligocene to mid Pliocene cooling (Stanley & Ruddiman, 1995). After the Middle Miocene climatic optimum (Zachos et al., 2001), this cooling trend probably led to a step-by-step breakdown of the original European-West African tropical province, as its northern limit contracted

southwards, and to the individualization of the present day Atlanto-Mediterranean warm temperate and subtropical bioprovinces.

The Mondego assemblage shows that, during mid Pliocene times, the Atlantic mollusk faunas of West Iberia, at this latitude, were already part of a different subtropical biogeographical unit (Silva, 2001), homologous to the Recent French-Iberian province of Raffi, Stanley & Marasti (1985). The Pliocene Western Iberian region was, as nowadays, characterized by cooler SSTs (Sea Surface Temperatures) than the more southern Mediterranean and West African areas (Silva, 2001). In the Early to mid Pliocene (corresponding to the faunistic Mediterranean Pliocene Molluscan Unit 1) everywhere in the Mediterranean tropical conditions prevailed (Monegatti & Raffi, 2001). Therefore, at least since the late Early Pliocene, South-Western Atlantic Iberia represented the northern boundary of what was left of the broad Miocene Euro-West African tropical province (Monegatti & Raffi, 2001; Silva 2001), by then merely encompassing the Atlantic Southern Iberian and West African coasts and the Mediterranean: the Mediterranean-West African Pliocene tropical province.

According to Monegatti & Raffi (2001), the mid Pliocene cooling event, registered around 3.0 Ma, has had a dramatic impact on Mediterranean Pliocene thermophilic taxa. This cooling event was responsible

for yet another geographic distribution contraction southwards and, this time, for the consequent individualization of the Mediterranean-Moroccan molluscan bioprovince and the narrowing of the Eastern Atlantic tropical area, generally speaking, to its present day limits (Figure 4). It seems that after this cooling event, *Spiricella unguiculus* disappeared from West Iberian coasts, and became restricted to the warmer southern province: the present day Mediterranean-Moroccan subtropical province.

CONCLUSION

The discovery of *Spiricella unguiculus* in the Pliocene of the Mondego Basin fills the gap up until now existing in the Oligocene to Recent geological distribution of the species.

Although the overall recorded occurrences of the species are rare, the Oligocene to Recent geographical distribution of *S. unguiculus* appears to have undergone a sharp southward contraction. This contraction is in accordance with the general biogeographic trend observed with other Atlanto-Mediterranean mollusk taxa (e.g., Silva et al., 2000; Monegatti & Raffi, 2001; La Perna et al. 2003), and supports the hypothesis of a Neogene Northern Atlantic cooling scenario (e.g., Stanley & Ruddiman, 1995; Monegatti & Raffi, 2001; Zachos et al. 2001).

Acknowledgments. The authors wish to acknowledge colleague Robert Marquet (Department of Palaeontology, Koninklijk Belgisch Instituut voor Natuurwetenschappen) for his help in the identification of the Portuguese *Spiricella* specimen.

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The Pliocene Cancellariidae (Mollusca: Gastropoda) of the Cubagua Formation (Cerro Negro Member) from Cubagua Island, with a new species from the Miocene Cantaure Formation, Venezuela

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Abstract. This is the first description of gastropod family Cancellariidae from the Lower Pliocene Cerro Negro Member of the Cubagua Formation from the Island of Cubagua, Venezuela. These deposits hold a rich and varied fauna of cancellariids, comprising at least nine species, plus a group which may contain more than one species, including two new taxa; *Cancellaria* (*Cancellaria*) *capeloi* nov. sp. and *Cancellaria* (*Massyla*) *cubaguaensis* nov. sp. Two new species are also described for the Lower Miocene Cantaure Formation of mainland Venezuela; *Cancellaria* (*Bivetiella*) *lugogonzalezorum* nov. sp., and *Cancellaria* (*Bivetopsia*) *herberti* nov. sp., increasing the number of cancellariids known from the Cantaure beds to 14. *Cancellaria* (*Pyrucilia*) *diadela* Woodring, 1970 is here considered a junior synonym of *Cancellaria* (*Pyrucilia*) *scheibei* Anderson, 1929. *Ventrilia kissimmeensis* Petuch, 1994 is here considered a synonym of *Trigonostoma* (*Ventrilia*) *ruckorum* (Petuch, 1994), as first revisers the latter name is chosen, the holotype of which is more characteristic of the species. The composition of the Neogene southern Caribbean cancellariid fauna is strongly paciphile, with most of the subgenera now restricted to the eastern Pacific. The Caribbean cancellariid fauna suffered a severe impoverishment following the uplift of the Panama Isthmus and closure of the Central American seaway, with only *Cancellaria* (*s. s.*) and *Cancellaria* (*Ventrilia*) of the larger-shelled taxa present in the Recent faunas.

INTRODUCTION

Numerous Neogene (including Quaternary, according to the latest revision of the chronostratigraphic scale, see Gradstein et al., 2004) fossiliferous deposits, rich in molluscan fossils, outcrop along or adjacent to the northern Caribbean coast of Venezuela. The fossil assemblage of the better known deposits, such as the Lower Miocene Cantaure and the Lower Pliocene Punta Gavilán Formations, Falcón State, have been described (Rutsch, 1934; Jung, 1965), whilst others remain almost unknown.

The presence of fossils of molluscs on the Island of Cubagua, Nueva Esparta State, situated between the Island of Margarita to the North and the Araya Peninsula to the South, is known since at least the 1930s (Schilder, 1939). Ingram (1947) described two new species of *Cypraea*, *C. grahami* and *C. rugosa*, from the Neogene deposits of the island, Gibson-Smith (1973) described *Voluta cubaguaensis*, and Vokes (1990) a new *Haustellum* species, *H. mimiwilsoni*. This work is part of an ongoing project to monograph the Pliocene gastropod fauna of Cubagua Island (Landau, Capelo and Silva, in press).

Geological Setting

The geological units outcropping on Cubagua Island are the Cubagua Formation and Tortuga Formation (Padrón et al., 1993). The sediments of the Upper Miocene to Upper Pliocene Cubagua Formation cover the greater part of the island (Padrón et al., 1993). Bermúdez and Bolli (1969) originally recognized two members to the Cubagua Formation, Cerro Verde (lower member) and Cerro Negro (upper member), of which only the Cerro Negro Member is represented in the island, namely at Cañon de las Calderas (Padrón et al., 1993), which is the type section for the Cubagua Formation (Castro and Mederos, 1997). The total thickness of the Cerro Negro member at its type locality of Cerro Negro, western part of the Araya Peninsula is 22 m (Vignali, 1965), and has a stratigraphic range from Lower Pliocene to Upper Pliocene and possibly Pleistocene (Padrón et al., 1993). In the Cañon de las Calderas the exposed section of the upper member of the Cubagua Formation attains 82 m (Padrón et al., 1993). The Cerro Negro Member overlays conformably the Cerro Verde Member (Vignali, 1965; Bermúdez, 1966). For further information

on the stratigraphy of the Cubagua Formation in Cubagua and graphic columnar section of the Cañon de las Calderas see Padrón et al. (1993).

The Tortuga Formation was originally described from Tortuga Island and dated as Middle to Upper Pleistocene (Patrick, 1959; Bermúdez, 1966). Méndez (1997) considered the formation restricted to the nominate Island of Tortuga. Nevertheless, according to Padrón et al. (1993), the Tortuga Formation crops out in Cubagua, consisting of a sequence of Holocene siltstones and limestones, which discontinuously fringe the coastline.

Within the Cerro Negro Member, in Cubagua, the most fossiliferous locality is situated on the eastern side of the Cañon de las Calderas. In this locality, the fossiliferous section consists of about 2 m of poorly consolidated sands, just above a clayey apparently non-fossiliferous layer at the base of the section, approximately 4–5 m above sea level. The fossils look abundant, but are probably concentrated on the surface by erosion of the sandy matrix. In several arroyos the sandy fossiliferous layer is exposed vertically and the fossils are sparsely distributed. According to Padrón et al. (1993) this fossiliferous section is Lower Pliocene in age.

Within the fossiliferous layer the shells occur in poorly defined levels; the lowest is richest in bivalves, the middle level is the thickest and contains the greatest diversity of gastropod species, and the upper level containing an assemblage consisting almost entirely of shells of Turritellidae and Vermetidae. The fossils in all layers are relatively well-preserved, most shells showing some surface erosion, and the early whorls of gastropod shells are almost invariably missing.

On mainland Venezuela a second locality, also belonging within the Cubagua Formation, occurs at Cerro Barrigón, about 1 km south of the village of Araya on the westernmost Araya Peninsula (see Padrón et al., 1993 and Jung, 1989 for location map). According to Vignali (1965) the Cubagua formation at Cerro Barrigón cannot be subdivided into its members the Cerro Verde and Cerro Negro. However, both Gibson-Smith and Gibson-Smith (1974) and Jung (1989) positioned the type locality of *Strombina arayana* Gibson-Smith and Gibson-Smith, 1974 in the Cerro Negro Member. We would agree with Gibson-Smith and Gibson-Smith (1974) in that the Cerro Negro Member can be clearly distinguished from the underlying Cerro Verde Member at Cerro Barrigón, where it consists of a lower level of fine, poorly consolidated sands (type bed for *S. arayana*), and an upper level of coarser, more consolidated sediments, in which the fossils are less well preserved. Both have a rich fossil molluscan assemblage, very similar to that found at Cañon de las Calderas on Cubagua Island.

The Lower Pliocene gastropod assemblage encountered in Cubagua indicates a tropical shallow-water, marine environment of normal salinity and with

a sandy substrate (Landau, Capelo and Silva, in press). These conclusions agree with Aguilera and Aguilera (2001: 733): 'the sediments of the lower part (of the Cubagua Formation, i.e., Cerro Verde Member) appear to have been deposited in deep water, and the upper part (i.e., Cerro Negro Member) in shallow tropical water.'

Biostratigraphic Setting

Bolli and Saunders (1985) proposed a zonal scheme for the Cenozoic of low latitudes developed in the areas of Trinidad and Venezuela, based on the assemblage of planktonic foraminifera. Five biostratigraphic zones and three subzones have been recognised in the Cubagua Formation. According to these authors, the assemblage of planktonic forams present in the Cerro Negro Member sediments at the Cañon de las Calderas indicates placement in the *Globorotalia margaritae* Zone of Bolli and Bermúdez (1965).

The Cubagua Formation ranges from the lower part of the Upper Miocene to the lower part of the Upper Pliocene, from Zone NN10, of *Discoaster calcaris* up to Zone NN17, of *Discoaster pentaradiatus* (Castro and Mederos, 1997). The *Gr. margaritae* Zone corresponds to the Lower Pliocene (Bolli and Saunders, 1985). Aguilera et al. (2001) in their work on the fish fauna of the Cubagua Formation used a preliminary age of 4.2 Ma (Lower Pliocene) throughout their paper, based on the median value of the age ranges of planktonic foraminifera obtained from all sampled areas. In the Cañon de las Calderas section the fossiliferous beds lie almost at the very base of the stratigraphic section, and are dated as Lower Pliocene by Padrón et al. (1993).

MATERIAL AND METHODS

The material described herein was collected in 2005 and 2006 on Cubagua Island and 2006 on the Araya Peninsula. Field sampling was conducted with the collaboration and field support of the Estación de Investigaciones Marinas de Margarita (EDIMAR), Fundación La Salle de Ciencias Naturales, Venezuela, which kindly put its facilities at our disposal, and are the result of an ongoing collaboration between the Fundación La Salle and the Department of Geology of the Faculty of Sciences of the Lisbon University for the study of the Pliocene Cubagua Island malacological assemblages.

The types are deposited in the Museo de la Estación de Investigaciones Marinas de Margarita, EDIMAR (EDIMAR coll.), in the Type Collection in the Invertebrate Paleontology Division of the Florida Museum of Natural History (FLMNH) at the University of Florida (UF). Other specimens figured

are in the Bernard Landau collection, Portugal (BL coll.).

SYSTEMATIC PALAEOONTOLOGY

Superfamily Cancellarioidea Forbes & Hanley, 1851

Family Cancellariidae Forbes & Hanley, 1851

Subfamily Cancellariinae Forbes & Hanley, 1851

The classification adopted here is according to Harasewych & Petit in Beesley et al. (1998) and Jung and Petit (1990). Most current workers (Ponder and Warén, 1988; Petit and Harasewych, 2005; Bouchet and Rocroi, 2005) follow Ponder (1973) in regarding Cancellarioidea as a superfamily within the Neogastropoda. More recently Kantor and Harasewych (1992) reported similar modifications in the anterior alimentary system of the muricoidean family Volutomitridae and suggested a re-assessment of the taxonomic rank and systematic position of the Cancellarioidea. Rosenberg et al. (1994) suggested the Cancellariidae originated within the Muricoidea on the basis of RNA sequence data.

Genus *Cancellaria* Lamarck, 1799

Subgenus *Cancellaria* Lamarck, 1799

Cancellaria (*Cancellaria*) *capeloi* nov. sp.

Figures 1–6

Dimensions and material: Holotype; MOBR-M-3359, 22.8 mm (EDIMAR coll.).

Other material: Paratype 1, height, 30.9 (BL coll.); paratype 2, height, 24.6 mm MOBR-M-3360 (EDIMAR coll.); paratype 3, UF 116699, height 26.6 mm; paratype 4, height, 20.6 mm (BL coll.), 12 further specimens, maximum height 32.7 mm (BL coll.).

Etymology: For our colleague Juan Carlos Capelo, malacologist of the Estación de Investigaciones Marinas de Margarita, EDIMAR, Fundación La Salle de Ciencias Naturales, Venezuela, without whose support and enthusiasm this work would not have been possible.

Type locality: Cañon de las Calderas, Cubagua Island, Nueva Esparta State, Venezuela.

Type section: Cerro Negro Member, Cubagua Formation, Lower Pliocene.

Diagnosis

A small to medium-sized *Cancellaria* s.s., with a somewhat scalate spire, narrowly canaliculated suture, medium mesh reticulate sculpture with the axial

component very slightly stronger, three non-bifurcate columellar folds, a well developed narrow siphonal fasciole and relatively broad umbilicus.

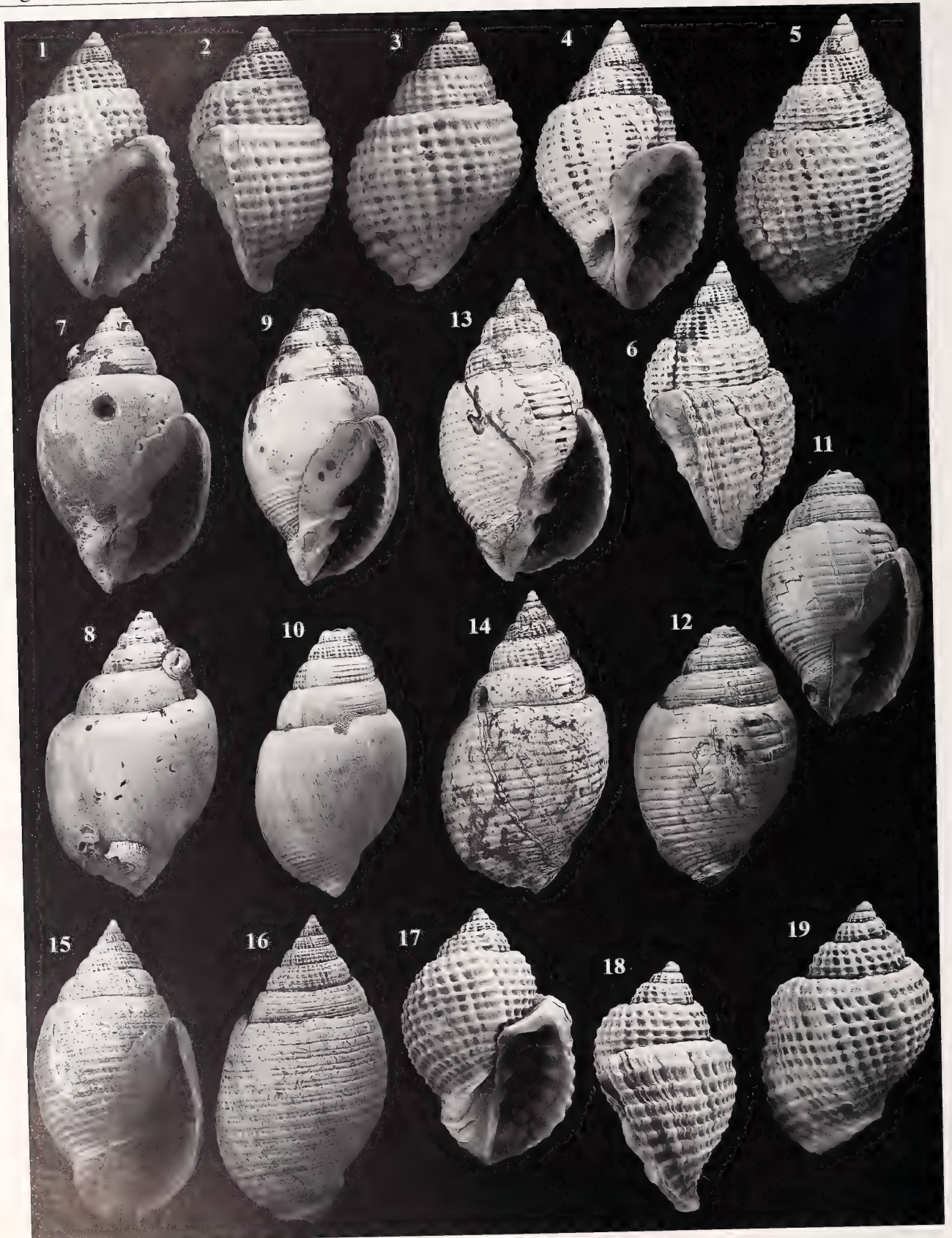
Description

Shell small to medium-sized, solid, ovate, with a medium mesh reticulate sculpture, of which the axial component is slightly stronger. Protoconch missing in all specimens. Teleoconch consists of 4.5–5 weakly convex whorls, with the periphery at the abapical suture. Suture deeply impressed and narrowly canaliculated, giving the spire a somewhat scalate appearance. Sculpture on first teleoconch whorls eroded in all specimens. On the third whorl spiral sculpture consists of five subequal cords, slightly narrower than their interspaces. Axial sculpture consists of about 22 strongly prosocline cords, slightly narrower than their interspaces. The spiral sculpture overrides the axial ribs forming tubercles at the intersections, varices absent. Whorl surface covered by fine prosocline growth lines. Last whorl inflated, regularly convex, with twelve spiral cords above the siphonal fasciole, 26–30 axial ribs, and weakly constricted behind the fasciole. Aperture approximately 50% of total height, sub-oval and elongate. Outer lip simple, not thickened by labial varix, weakly prosocline in profile, stromboid notch absent. Lip with a crenulate edge, strongly and deeply lirate within, but the lirae do not extend to the outer edge. Anal canal poorly developed; siphonal canal short, narrow and slightly recurved. Columella bears three non-bifid folds, the adapical fold largest, overlying the siphonal fasciole. Parietal callus thin, adherent onto the ventral aspect of the last whorl, the whorl sculpture visible through the callus. Columella callus thicker, detached forming the medial wall of the umbilical chink. Siphonal fasciole well developed, narrow, rounded and elevated, bearing four or five spiral cords. Umbilical chink relatively wide and deep for genus.

Discussion

Although *Cancellaria* s.s. usually has a bifid adapical columellar fold, some species characterized by shells lacking that feature, but possessing the other characters of the nominate subgenus, are considered to be part of the nominate subgenus. Several such species were so treated by Jung and Petit (1990).

Several American Neogene Caribbean taxa; *Cancellaria* (*Cancellaria*) *barretti* Guppy, 1866, *Cancellaria* (*Cancellaria*) *guppyi* Gabb, 1873, *Cancellaria* (*Cancellaria*) *petiti* Olsson, 1967, *Cancellaria* (*Cancellaria*) *acalypta* Woodring, 1970 are immediately distinguished from *C. (C.) capeloi* nov. sp. in having a clearly bifurcate adapical columellar fold. The shell of *Cancellaria (C.) harrisi* Maury, 1917, from the Upper



Miocene Cercado Formation of the Dominican Republic, which shows a bifid adapical fold, although only slightly so at its terminal portion, is similar in size and shape, but is more elongated and the whorls shouldered close to the suture. *C. epistomifera sathra* Woodring, 1973 (new name for *C. e. lipara* Woodring, 1970) (Woodring, 1973: 481) from the Upper Gatun Formation of Panama is similar to the new species with a scalate spire and slightly umbilicate, these features far more prominent in *C. (C.) capeloi* nov. sp., but differs in having a weakly bifid abapical fold, and being more constricted at the base. We do not consider *C. epistomifera sathra* to be a subspecies of the *C. epistomifera*, widespread in the Dominican Republic Neogene (Jung & Petit, 1990), which is quite different, with a non scalate spire, a far more globose last whorl and flaring outer lip with a deep stromboid notch.

Cancellaria (Cancellaria) dariena Toulou, 1909 is a *Cancellaria* s.s. with a shell showing a narrow, slightly bifid adapical fold. This species was described from the Gatun area of Panama, and is not particularly similar to *C. (C.) capeloi*, the greatest difference seen at the base, where *C. dariena* is far more constricted with the umbilicus poorly developed, also the posterior fold is much sharper and bifid.

Weisbord (1929, pl. 6, figure 8) figured a specimen as *Cancellaria dariena* Toulou, 1909 from the Tubará Group of Colombia, which is not conspecific with the Gatun taxon. The Colombian specimen seems to have a non-bifurcate adapical fold. Most of the Tubará specimens are stated by Weisbord (1929: 282) to have a thickened varix at the outer lip or "about the middle of the body whorl in back," a feature not seen in *C. (C.) capeloi*. Although the Tubará shell assigned to *C. dariena* is extremely close to *C. (C.) capeloi*, it has slightly fewer axial ribs, less evenly reticulated sculpture and the spire is less scalate.

Of the Lower Miocene species of *Cancellaria* s.s. with a non-bifid adapical fold, *Cancellaria (Cancellaria) rowelli* Dall, 1896 from the Baitoa Formation of the Dominican Republic has a shell with a taller spire, somewhat finer sculpture, the last whorl strongly constricted behind the siphonal fasciole and although the fasciole is also well developed, the umbilicus is

narrower than in *C. (C.) capeloi*. *Cancellaria (Cancellaria) hodsonae* Landau and Petit, 1997 from the Cantaure Formation of Venezuela is even more elongate, taller spired, with strong spiral sculpture at the shoulder.

Two further species with non-bifurcate columellar folds occur in the Upper Miocene Cercado Formation of the Dominican Republic; *Cancellaria (Cancellaria) mauryae* Olsson, 1922 and *Cancellaria (Cancellaria) juncta* Jung and Petit, 1990. Both have larger and thinner shells, with a more inflated body whorl, a much finer sculpture, a much less elevated the siphonal fasciole, and a very small umbilical chink. Weisbord (1962) described *Cancellaria torula* from the Lower Mare Formation, Middle Pliocene of Venezuela. The type material consisted of a single incomplete and very poorly preserved juvenile specimen. Weisbord (1962: 398) distinguished this mutilated *Cancellaria* shell from its congeners on the basis of a "strong, irregularly thickened, *Distorsio*-like ridge on the parietal wall." Gibson-Smith & Gibson-Smith (1979) placed *C. torula* in the synonymy of *C. reticulata* (Linnaeus, 1767) on the basis of the fact that the parietal ridge that Weisbord (1962) used to differentiate *C. torula* from *C. reticulata* and other *Cancellaria* s.s. was absent in an adult specimen but present in a juvenile collected by the Gibson-Smiths. They declared the ridge to be an "intermittent resting stage in the juveniles but is absent in the adults" (Gibson-Smith & Gibson-Smith, 1979: 26). This ridge is indeed present in juvenile shells of *C. reticulata*, and a trace of one is present in some adult specimens (Petit, personal observation). On the basis of the specimen illustrated by Weisbord (1962), it is impossible to say with any certainty what is meant by *C. torula*, however, the posterior ridge is finer than that seen in *C. capeloi* (although Weisbord's shell is probably juvenile), and the parietal ridge is not present in any of the Cubagua shells, even at the juvenile stage. The Gibson-Smith & Gibson-Smith (1979) Mare material of *Cancellaria (C.) torula* is not available but, based on sculpture visible on the type figure of *C. torula*, the specimen is unlikely to be conspecific with *C. reticulata*, and possibly closer to

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Figures 1–19. Figures 1–3. *Cancellaria (Cancellaria) capeloi* nov. sp. Holotype; MOBR-M-3359 (EDIMAR coll.), Locality 1, Cañon de las Calderas. Height 22.8 mm. Figures 4–6. *Cancellaria (Cancellaria) capeloi* nov. sp. paratype; BL coll., Locality 1, Cañon de las Calderas. Height 30.9 mm. Figures 7–8. *Cancellaria (Cancellaria)* sp. Specimen 1. BL coll., Lower sandy bed, Cerro Barrigón, Araya Peninsula, Venezuela. Height 44.9 mm. Figures 9–10. *Cancellaria (Cancellaria)* sp. Specimen 2. BL coll., Lower sandy bed, Cerro Barrigón, Araya Peninsula, Venezuela. Height 47.4 mm. Figures 11–12. *Cancellaria (Cancellaria)* sp. Specimen 2. BL coll., Upper bed, Cerro Barrigón, Araya Peninsula, Venezuela. Height 41.2 mm. Figures 13–14. *Cancellaria (Cancellaria)* sp. Specimen 2. BL coll., Lower sandy bed, Cerro Barrigón, Araya Peninsula, Venezuela. Height 37.1 mm. Figures 15–16. *Cancellaria (Cancellaria)* sp. Specimen 2. BL coll., Locality 1, Cañon de las Calderas. Height 46.2 mm. Figures 17–19. *Cancellaria (Bivetiella) lugogonzalezorum* Holotype; MOBR-M-3361 (EDIMAR coll.), Casa Cantaure, east of San Jose, Paraguaná Peninsula, Falcón State, Venezuela, Cantaure Formation, Lower Miocene.

C. capeloi. Due to the fact that *C. torula* has been formalized on a single incomplete and very poorly preserved juvenile specimen, we consider the Weisbord taxon to be a *nomen dubium*. Moreover, few species are common to both Mare and Cubagua. The supposed conspecificity of *C. torula* and *C. reticulata* argues against uniting it with *C. capeloi* which cannot be confused with *C. reticulata*.

Distribution

Lower Pliocene: Cubagua Formation, Cubagua Island, Venezuela.

Cancellaria (Cancellaria) ssp.

We have five shells from the Cerro Negro Member of the Cubagua Formation tentatively placed in the nominate subgenus; all have a bifurcated posterior columellar fold except for one (Figures 7–8). One is from Cañon de las Calderas (Specimen 5; Figures 15–16) and the other four from Cerro Barrigón on the Araya Peninsula, three from the 'lower bed' (Specimens 1, 2 and 4; Figures 7–8, 9–10 and 13–14), one from the 'upper bed' (Specimen 3; figure 11–12).

All five specimens are slightly different requiring a short description of the salient features of each;

Specimen 1 (Figures 7–8)

Shell ovate, spire mid-height, strongly scalate. Six teleoconch whorls preserved, shouldered, last whorl strongly shouldered; axial sculpture consisting of prosocline ribs, 20 on the fourth whorl, weakening abapically, obsolete after the first quarter of the penultimate whorl; spiral sculpture of primary cords obsolete after the first quarter of the penultimate whorl, persisting only on the base.

Specimen 2 (Figures 9–10)

Shell ovate-fusiform, spire tall and somewhat scalate. Four teleoconch whorls preserved, somewhat shouldered; axial sculpture consisting of close-set prosocline ribs, 29 on the second preserved whorl (probably the fourth whorl), weakening abapically, obsolete after the first quarter of the penultimate whorl; spiral sculpture of primary cords obsolete on the second half of the penultimate whorl, persisting only on the base.

Specimen 3 (Figures 11–12)

Shell ovate-fusiform. Protoconch worn, but consisting of at least two elevated whorls. Six teleoconch whorls, not shouldered; axial sculpture consisting of close-set prosocline ribs, 26 on the fourth whorl,

weakening abapically, obsolete on the second half of the penultimate whorl; spiral sculpture of primary cords only strongly developed throughout.

Specimen 3 (Figures 13–14)

Shell ovate-fusiform. Three teleoconch whorls preserved, weakly shouldered; axial sculpture consisting of close-set prosocline ribs, 28 on the first preserved whorl (probably the fourth whorl), weakening abapically, obsolete on the last quarter of the penultimate whorl; spiral sculpture of primary cords developed throughout, with a tendency for the cords mid-whorl to subdivide.

Specimen 5 (Figures 15–16)

Shell ovate-fusiform. Protoconch worn. Seven teleoconch whorls, not shouldered; axial sculpture consisting of close-set prosocline ribs, 47 on the fourth whorl, weakening abapically, but persisting onto the first half of the last whorl; spiral sculpture of primary and secondary cords strongly developed throughout.

Although the sculpture weakens considerably on the last whorl of most of these five shells, as seen in the subgenus *Pyrucilia*, the posterior columellar fold is bifid in four of the five shells and not large and broadly divided, giving the appearance of an additional fold, as in *Pyrucilia* (Jung and Petit, 1990).

Compared to other Caribbean taxa with fusiform rather than pyriform shells; *C. (Pyrucilia?) uva* Jung and Petit, 1990 from the Lower Miocene, Baitoa Formation of the Dominican Republic has closely packed axial cords on the early whorls, similar to our specimen 5, but the axial ribs disappear at the end of the penultimate whorl and the spiral sculpture is subobsolete on the last whorl, the shell shape is similar to our specimen 1. *Cancellaria (P?) laevescens* Guppy, 1866 is closely similar in shell shape to our specimen 1, with a similar number of ribs on the fourth whorl as our specimens 2–4, which persist until the end of the penultimate whorl. All the Pliocene Pacific species from Ecuador; *C. (P?) lacondamini*, *C. (P?) picta*, *C. (P?) telemba* all Olsson, 1964 have shells with lower-spires and more globose last whorls.

Our series of shells is similar to the Recent eastern Pacific group comprising *C. (C.) obesa* Sowerby, 1832 and *C. (C.) ovata* Sowerby, 1832, our broader shells with smooth last whorls similar to the former, the more fusiform shells with spiral sculpture persisting on the last whorl to the latter. The Pacific Pleistocene *C. (C.) coronadoensis* Durham, 1950, which is not consistently different from the Recent Pacific *C. (C.) obesa* Sowerby, 1832, is similar to our specimen 1, but the axial sculpture is much finer, and confined to the early teleoconch whorls.

With the scant material from the Cubagua Formation available to us we are unable to conclude if we are dealing with a single variable taxon or several distinct sympatric species. Nevertheless, these shells again reflect the strongly paciphile character of the Cubagua cancellarid fauna.

Subgenus *Bivetiella* Wenz, 1943

Cancellaria (Bivetiella) lugogonzalezorum nov. sp.

Figures 17–19

Cancellaria (Cancellaria?) lavelana H. K. Hodson - Jung, 1965, p. 550, pl. 75, Figures 5–6 (non H. K. Hodson in Hodson and Hodson, 1931).

Dimensions and material: Holotype; MOBR-M-3361, height, 17.6 mm (EDIMAR coll.).

Other material: Paratype1 MOBR-M-3362 (EDIMAR coll.), height, 17.6 mm; paratype 2, UF 116700, height, 16.3 mm; paratype 3, height, 16.5 mm (BL coll.), plus 29 further paratypes (BL coll.).

Etymology: For the family Lugo Gonzalez of San Jose de Cocodite, Paraguaná Peninsula, Venezuela, owners of the Cantaure property, for their generous hospitality during our numerous trips.

Type locality: Casa Cantaure, east of San Jose de Cocodite, Paraguaná Peninsula, Falcón State, Venezuela.

Type section: Cantaure Formation, Lower Miocene.

Description

Shell small, solid, ovate, with a fine mesh reticulate sculpture, the axial component slightly stronger. Protoconch consists of about three smooth, strongly convex whorls, with a small nucleus. Junction with teleoconch sharply delimited by a prosocline scar. Teleoconch consists of four convex whorls, with the periphery at the abapical suture. Suture deeply impressed and narrowly canaliculated. Sculpture consists of prosocline rounded axial rib, about half the width if their interspaces, 9–14 on the first teleoconch whorl, 17–22 on the penultimate. Weakly developed varices present at about 120° intervals. Spiral sculpture consists of rounded spiral cords, about half the width if their interspaces, three on the first teleoconch whorl, 5–6 on the penultimate. The two adapical cords on the later adult whorls are more closely set than the remaining cords. The spiral sculpture overrides the axial ribs forming small tubercles at the intersections. Whorl surface covered by fine prosocline growth lines. Last whorl strongly inflated, regularly convex, with 12–14 spiral cords above the siphonal fasciole, about 35

axial ribs and moderately constricted behind the fasciole. Aperture approximately 50% of total height, sub-oval and elongate. Outer lip simple, not thickened by labial varix, slightly flared abapically, strongly prosocline in profile, stromboid notch absent. Lip with a crenulate edge, bearing six strong denticles a short distance inside the lip, which continue as lirae within. Anal canal poorly developed; siphonal canal short, narrow and slightly recurved. Columella bears three bifid folds, the adapical fold largest. Parietal callus thin, adherent onto the ventral aspect of the last whorl, the whorl sculpture visible through the callus. Columella callus thicker, detached forming the medial wall of the umbilical chink. Siphonal fasciole well developed, rounded and elevated, bearing three cords. Umbilical chink relatively wide for genus.

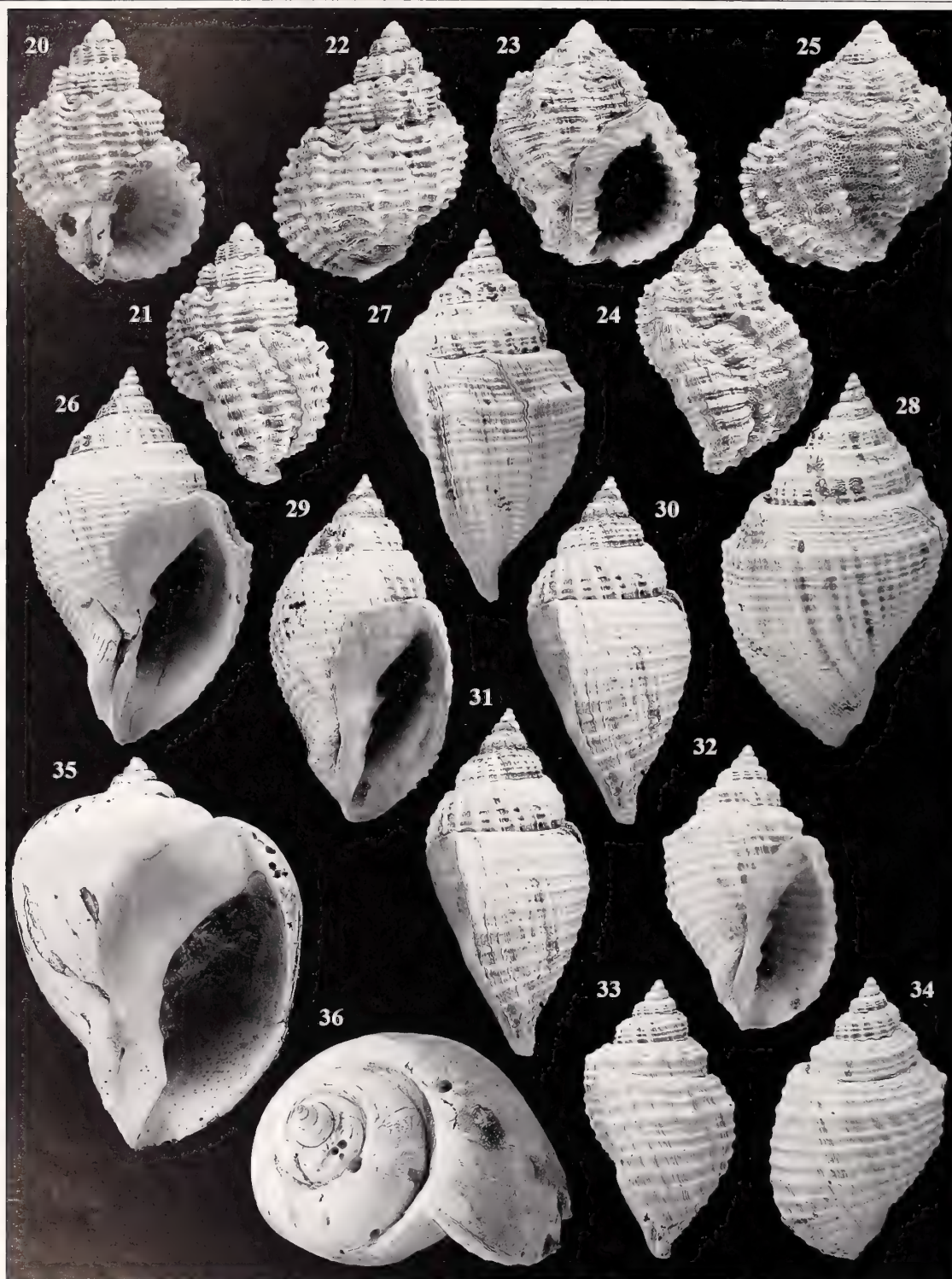
Discussion

The holotype of *C. (B.) lugogonzalezorum* nov. sp. is almost certainly conspecific with the shell illustrated by Jung (1965) as *Cancellaria (Cancellaria?) lavelana* H. K. Hodson. However, Hodson's (1931, pl. 24, figure 12) shell is a species of *Massyla* H. and A. Adams, 1854. Landau and Petit (1996) discussed and renamed some of the Cantaure cancellarids described by Jung (1965).

Cancellaria (Bivetiella) lugogonzalezorum nov. sp. again illustrates the difficulty in placing Caribbean Neogene species of the Cancellariidae neatly within subgenera, and this species is herein tentatively placed within the subgenus *Bivetiella*. The shell has weak varices and bifid second and third folds, seen in some species within the subgenus *Bivetiella*, but the adapical fold is also bifid. A stromboid notch, a typical feature of *Cancellaria* s.s., is not present. The outer lip is slightly flared abapically, but not as clearly everted as in most *Bivetiella* species. In view of the small size and relatively inflated last whorl we have opted for the subgenus *Bivetiella*.

C. (B.) lugogonzalezorum nov. sp. shows great variability in shell features. In gerontic specimens the last whorl is more elongated, the outer lip slightly more flared. The reticulate sculpture is of somewhat variable mesh size, with a tendency in some specimens to have a few cords crowded together below the adapical suture, followed by one or two cords more widely spaced than the rest, whilst in others the reticulation is regular. The height of the spire, width of the umbilicus and strength of the labral denticulation are all variable as are the folds, clearly bifid to incipiently so.

Despite this great variability, the shells of this new species are very characteristic, being the smallest in the subgenus, and the intermediate features outlined above distinguish them from other members of *Cancellaria* and *Bivetiella*. We draw particular attention to the strongly prosocline outer lip profile.



Figures 20-37. Figures 20-22. *Cancellaria (Bivetopsia) pachia* M. Smith, 1940. BL coll., Locality 1, Cañon de las Calderas. Height 24.6 mm. Figures 23-25 *Cancellaria (Bivetopsia) herberti* nov. sp. Holotype; MOBR-M-3419 (EDIMAR coll.), Casa Cantaure, east of San Jose, Paraguaná Peninsula, Falcón State, Venezuela, Cantaure Formation, Lower Miocene, Height 18.8 mm. Figures 26-28. *Cancellaria (Euclia) codazzii* Anderson, 1929. BL coll., Locality 1, Cañon de las Calderas. Height 41.9 mm. Figures 29-31. *Cancellaria (Euclia) leuzingeri* Rutsch, 1934. BL coll., Locality 1, Cañon de las Calderas. Height 44.2 mm. Figures 32-34. *Cancellaria (Euclia) montserratensis* Maury, 1925. BL coll., Locality 1, Cañon de las Calderas. Height 37.0 mm. Figures 35-37. *Cancellaria (Pyrucilia) scheibei* Anderson, 1929. BL coll., Locality 1, Cañon de las Calderas. Height 49.9 mm.

Cancellaria (*B.*) *lugogonzalezorum* is superficially similar to *C.* (*C.*) *capeloi*, but is immediately distinguished by the bifid columellar folds and strongly prosocline outer lip.

With the description of this new species, and the record of an undescribed *Cancellaria* (*Bivetopsia*) nov. sp. (Figures 23–25), the number of cancellarids known from the Lower Miocene Cantaure Formation is increased to 14 (see Landau and Petit, 1996).

Distribution

Lower Miocene: Cantaure Formation, Paraguaná Peninsula, Falcón State, Venezuela.

Subgenus *Bivetopsia* Joussemae, 1887

Cancellaria (*Bivetopsia*) *pachia* M. Smith, 1940

Figures 20–22

Cancellaria pachia M. Smith, 1940, p. 45, pl. 2, figure 2.
non *Bivetopsia pachia* (M. Smith, 1940) - Petuch, 1994, p. 222,
pl. 90, figure C.

Material and dimensions: Maximum height 25.9 mm. 14 specimens Cañon de las Calderas, Cubagua Island; 3 specimens 'upper bed,' Cerro Barrigón, Araya Peninsula (BL coll.).

Discussion

The characteristics of the subgenus *Bivetopsia* Joussemae, 1887 were discussed by Jung and Petit (1990), similar to *Bivetiella* Wenz, 1943, but usually smaller shelled, without a stromboid notch at the outer lip, and the last whorl strongly constricted behind a well developed siphonal fasciole.

Although Jung and Petit (1990) cited *Bivetopsia pachia* (M. Smith, 1940) as a subspecies of *B. moorei* (Guppy, 1866) they are separate species. *C.* (*B.*) *moorei* has a shell with a more attenuate profile lacking the strong shoulder and thickened out lip of *C.* (*B.*) *pachia*. However, the major and most easily noted difference is the presence of wider spiral cords on the shells of *C.* (*B.*) *pachia*, all of which are bifurcated by a deep narrow groove, a feature not prominent in other species. *Cancellaria* (*B.*) *plectilis* (Jung and Petit, 1990) has even heavier spiral cords with multiple grooves. The Recent species *Cancellaria* (*Bivetopsia*) *rugosa* (Lamarck, 1822), distinguished by its rounded form and low sculpture, also has grooves in the spiral cords but they are neither as pronounced nor prominent as they are in the shells of other species and are sometimes absent on most of the cords. The specimen figured by Petuch (1994, pl. 90, figure C) as *Bivetopsia pachia* does not correspond to that species and cannot be clearly

identified from the illustration, but it appears to be a shell of either *C.* (*B.*) *rugosa* or of a very closely related unnamed species.

The subgenus *Bivetopsia* is American, the few known species confined to the Neogene of Florida, the Caribbean and Ecuador, and the Recent fauna of the Caribbean and the Panamic-Pacific provinces. Cahuzac et al. (2004) suggested *Scalptia spinosa* (Gratoloup, 1827) from the Lower Miocene of Landes, France, had some features of this taxon, but the shell shape and aperture characteristics are not those of *Bivetopsia*. The group first appeared in the Lower Miocene Cantaure Formation of Venezuela, represented by *Cancellaria* (*Bivetopsia*) *herberti* nov. sp. (Figures 23–25), which differs from both *C.* (*Bivetopsia*) *pachia* and *C.* (*B.*) *moorei* in being smaller, squatter, with a more depressed spire, with fewer axial ribs, a similar number of spiral cords, but with a secondary cord in some of the interspaces and the suture is less depressed and not canaliculated. The Cantaure specimen is more similar in shape to the Recent *C.* (*B.*) *chrysostoma* Sowerby, 1832, type species of *Bivetopsia*, but the umbilicus is wider and the suture again somewhat canaliculated in the Recent species. The presence of *C.* (*B.*) *pachia* in Cubagua is interesting, making it one of the most long-lived Caribbean Neogene cancellarids, Early Pliocene to Pleistocene, with a wide geographical distribution. Only *Extractrix hoerlei* Olson, 1967 has a wider distribution in the Pliocene, reported from the Lower Pliocene of Punta Gavilán, mainland Venezuela (Jung, 1977) and the Lower-Middle Pliocene of Virginia, USA (Campbell, 1993).

Distribution

Lower Pliocene: Cubagua Formation, Cubagua Island, Venezuela.

Plio-Pleistocene: Florida (M. Smith, 1940).

Cancellaria (*Bivetopsia*) *herberti* nov. sp.

Figures 23–25

Dimensions and material: Holotype; Holotype; MOBR-M-3419, 18.8 mm (EDIMAR coll.).

Other material: Paratype, height, 19.0 mm (BL coll.).

Etymology: For Gregory Herbert of the University of South Florida in recognition of his wonderful work on Neogene Caribbean taxonomy.

Type locality: Casa Cantaure, east of San José de Cocodite, Paraguaná Peninsula, Falcón State, Venezuela.

Type section: Cantaure Formation, Lower Miocene.

Description

Shell small, solid, ovate, squat, with a predominantly axial sculpture. Protoconch consists of about three and a half smooth, strongly convex whorls, with a small nucleus. Junction with teleoconch sharply delimited by a prosocline scar. Teleoconch consists of three and a half convex whorls, with the periphery at the abapical suture. Suture deeply impressed and undulating. Sculpture on the first teleoconch whorl somewhat eroded. Second teleoconch whorl bears 12 prosocline axial ribs, of very irregular strength, about half the width of their interspaces. Last whorl bears eight, every second or third rib thickened into a varix. Spiral sculpture consists of six narrow, elevated spiral cords on the first and second whorls, with secondary threads intercalated towards the end of the second whorl. Last whorl with 12 primary spiral cords, secondary threads in some, but not all interspaces, some of the primary cords mid-whorl weakly bifid. On the last whorl the sculptural intersections at the shoulder are developed into small, horizontally-elongated, adapically-pointing rounded tubercles, giving the whorl a somewhat shouldered appearance. Whorl surface covered in prosocline growth lamellae, giving the shell a somewhat scabrous appearance. Last whorl globose, squat, moderately constricted behind the fasciole. Aperture approximately 60% of total height, sub-oval and elongate. Outer lip thickened by a broad labial varix, flared abapically, prosocline in profile and angled at the rather narrow, but distinct stromboid notch. Lip with a crenulated edge, strongly and deeply lirated within, 13 lirae, the abapical lirae ending almost at the lip edge in a slightly thickened denticle. Columella bears three non-bifid folds, the adapical fold largest. Columellar and parietal calluses strongly thickened, sharply delimited, moderately expanded and adherent onto the ventral aspect of the last whorl. The entire callus is covered in numerous irregular folds and tubercles. Siphonal canal damaged. Siphonal fasciole well developed, rounded and elevated, bearing six cords. Umbilical chink present, of average size for genus.

Discussion

Although this species is represented only by the holotype with a damaged siphonal canal, and a sub-adult damaged specimen (paratype 1, BL coll.), it is distinctive enough to be certain it is different from all other known *Bivetopsia* species. For comparison with other related species see above.

Distribution

Lower Miocene: Cantaure Formation, Paraguaná Peninsula, Falcón State, Venezuela.

Cancellaria (Euclia) codazzii Anderson, 1929

Figures 26–28

- Cancellaria codazzii* Anderson, 1929, p. 116, pl. 14, Figures 4–7; Barrios, 1960, p. 291, pl. 11, figure 5.
Cancellaria karsteni Anderson, 1929, p. 114, pl. 10, Figures 7–9.
Cancellaria hettneri Anderson, 1929, p. 114, pl. 10, Figures 5–6.
Cancellaria (Euclia) cf. *codazzii* Anderson - Jung, 1969, p. 541, pl. 58, figure 8.
Cancellaria (Euclia) codazzii Anderson - Woodring, 1970, p. 339, pl. 54, Figures 3, 4, 7, 8, 11, 12.

Material and dimensions: Maximum height 41.9 mm. 6 specimens Cañon de las Calderas, Cubagua Island (BL coll.).

Discussion

As discussed by Woodring (1970), the shells of this species are very variable, with the angulation at the shoulder of the last whorl and the spines more or less developed. Woodring (1970) considered *C. (E.) karsteni* Anderson and *C. (E.) hettneri* Anderson to be synonyms of *C. (E.) codazzii*. As first reviser he selected the name *C. codazzii* as the senior synonym, considering the other two nominal species to represent variability extremes. Woodring also included in his synonymy *C. (E.) maldonadoi* Olsson, 1964 from the Pacific Upper Miocene Angostura Formation of Ecuador. That synonymy was not accepted by Jung & Petit (1999) as *C. (E.) maldonadoi* has a rounded body whorl whereas the shells of *C. (E.) codazzii* have a sharp shoulder with a flat or concave area posterior to the shoulder. Our specimens from Cubagua have a flat or concave shoulder posterior to the angled shoulder and match the type specimen of *C. (E.) codazzii*.

The subgenus *Euclia* H. and A. Adams, 1854 is characterized by having swollen axial ribs on the last whorl with a tendency to form nodules at the shoulder. Both *Euclia* and *Pyruculia* Olsson, 1932 represent species groups which were present in the Neogene Caribbean but are now restricted to the Pacific. In this particular case the lineage starts in the Early Miocene with *C. (E.) werenfelsi* Jung, 1965 from the Cantaure Formation of Venezuela. This is a species with a relatively small, elongated shell, with fine axial sculpture and relatively well-developed spines at the shoulder. *Cancellaria (E.) codazzii* is then present in both the Atlantic and Pacific in the Late Miocene giving rise to the Pacific Tropical American species of *Euclia* of which *C. (E.) balboae* Pilsbry, 1931 is the most similar, but differs in having fewer axial ribs on the spire whorls (Woodring, 1970). The shell of the more common Pacific Pleistocene to Recent *C. (E.) cassidiformis* Sowerby, 1832 is larger, more spinose and has angular spire whorls as well on the last whorl.

Distribution

Upper Miocene: Gatun Formation, Panama (Woodring, 1970).

Lower Pliocene: Cubagua Formation, Cubagua Island, Venezuela; Tubará Group, northern Colombia (Anderson, 1929; Barrios, 1960); Melajo Clay Member of Springvale Formation, Trinidad (Jung, 1969).

Cancellaria (Euclia) leuzingeri Rutsch, 1934

Figures 29–31

Cancellaria reticulata leuzingeri Rutsch, 1934, p. 89, pl. 7, Figures 10–11, pl. 8, Figures 1, 2, 5.

Material and dimensions: Maximum height 50.1 mm. 11 specimens (BL coll.), 10 specimens (EDIMAR coll.), Cañon de las Calderas, Cubagua Island; 8 specimens 'lower bed,' Cerro Barrigón, Araya Peninsula (BL coll.).

Discussion

Cancellaria (Euclia) leuzingeri Rutsch, 1934 is common at both its type locality, at Punta Gavilán, and at Cañon de las Calderas, but has not been found outside of Venezuela. Originally described as a subspecies of *Cancellaria reticulata* (Linnaeus, 1767), the affinity between the two is superficial. The adapical columellar fold in *C. reticulata* is bifurcate, a character of *Cancellaria* s.s. The form of the columellar folds and the shell outline clearly place *C. leuzingeri* in the subgenus *Euclia*. The species is very close to the Recent *C. (E.) laurettae* Petit and Harasewych, 1998 from bathyal depths in the Golfo de Chiriqui, Panama (Pacific). A characteristic of the shells of most species of the subgenus is the "stretched out" shape of the aperture.

Petit and Harasewych (1998, p. 113) listed the Cenozoic and Recent species of *Euclia* known from Panamic faunas, as well as Cenozoic species from the Caribbean, where the subgenus no longer occurs (i.e., a paciphile genus). Unfortunately *C. (E.) leuzingeri* was omitted from that list.

Distribution

Lower Pliocene: Cubagua Formation, Cubagua Island, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (Rutsch, 1934).

Cancellaria (Euclia) montserratensis Maury, 1925

Figures 32–34

Cancellaria montserratensis Maury, 1925, p. 346, pl. 35, Figures 6, 8; Rutsch, 1942, p. 163, pl. 9, figure 7.

Cancellaria epistomifera Guppy - Maury, 1925, p. 345, pl. 35, figure 7 (non *C. epistomifera* Guppy, 1876).

Cancellaria springvaleensis Mansfield, 1925, p. 31, pl. 2, figure 12.

Cancellaria (Cancellaria) couvana Vokes, 1938, p. 20, figure 21.

Cancellaria (Euclia) montserratensis Maury - Jung, 1969, p. 539, pl. 58, Figures 6–7.

Material and dimensions: Maximum height 41.2 mm. 17 specimens (BL coll.), 8 specimens (EDIMAR coll.), Cañon de las Calderas, Cubagua Island; 2 specimens 'upper bed,' Cerro Barrigón, Araya Peninsula (BL coll.).

Discussion

Cancellaria (Euclia) montserratensis Maury, 1925 is one of the commoner cancellarids found at Cañon de las Calderas. It is easily distinguished from *Cancellaria (Euclia) codazzii* Anderson, 1929, which has a shell with a less scalate spire, finer spiral sculpture, less angular whorls, with the shoulder placed further from the suture. Maury (1925) compared it to *Cancellaria harrisi* Maury, 1917, from the Miocene of the Dominican Republic, but this is a much smaller shell with finer sculpture.

Distribution

Lower Pliocene: Cubagua Formation, Cubagua Island, Venezuela; Tubará Group, northern Colombia (Anderson, 1929; Barrios, 1960); Savaneta Glauconitic Sandstone Member and Melajo Clay Member of Springvale Formation, Trinidad (Maury, 1925; Mansfield, 1925; Vokes, 1938; Rutsch, 1942; Jung, 1969).

Subgenus *Pyrucelia* Olsson, 1932

Cancellaria (Pyrucelia) scheibei Anderson, 1929

Figures 35–37

Cancellaria scheibei Anderson, 1929, p. 115, pl. 10, Figures 1–4.

Cancellaria (Pyrucelia) diadela Woodring, 1970, p. 338, pl. 53, Figures 7, 9.

Material and dimensions: Maximum height 77.2 mm. 9 specimens (BL coll.), 4 specimens (EDIMAR coll.), Cañon de las Calderas, Cubagua Island; 2 specimens 'upper bed,' Cerro Barrigón, Araya Peninsula (BL coll.).

Discussion

Cancellaria (Pyrucelia) scheibei Anderson, 1929 is not uncommon at Cañon de las Calderas, where the shells reach a large size, but are rarely complete. Although the deep sutural canal is not evident in the figure of the holotype (Anderson, 1929, pl. 10, Figures 1–2), our specimens match the original description, also having weak axial sculpture confined to the first two to three

teleoconch whorls. Woodring (1970) described a very close species based on a single shell from the upper part of the Gatun Formation of Panama, *Cancellaria* (*Pyrucelia*) *diadela*, said to differ in having a lower spire and a more angular last whorl. The height of the spire and strength and position of the shoulder is rather variable in the Cubagua specimens and, therefore, we consider the latter a junior synonym of *C. (P.) scheibei*.

Jung and Petit (1990) discussed the characters of the subgenus *Pyrucelia*, and stressed that only the species with a pyriform shell could be assigned to it with certainty. *Cancellaria* (*Pyrucelia*) *scheibei* is somewhat unusual and can easily be distinguished from its congeners by the extremely wide and deeply channelled sutural canal. The *Pyrucelia* s.s. species group seems to have appeared in the Late Miocene simultaneously on both sides of the Central American Seaway, and survived in the Atlantic only into the earliest Pliocene. Today it is represented in the Pacific by two species; *C. (P.) solida* Sowerby, 1832 and *C. (P.) bulbulus* Sowerby, 1832. *Cancellaria* (*P.*) *solida* is the most similar, but lacks the deep sutural canal.

Distribution

Lower Pliocene: Cubagua Formation, Cubagua Island, Venezuela; Tubará Group, northern Colombia (Anderson, 1929); Gatun Formation, Panama (Woodring, 1970).

Subgenus *Massyla* H. and A. Adams, 1854

Cancellaria (*Massyla*) *cubaguaensis* nov. sp.

Figures 38–44

Dimensions and material: Holotype; MOBR-M-3363, height, 25.9 mm (EDIMAR coll.).

Other material: Paratype 1 24.6 mm MOBR-M-3364 (EDIMAR coll.); paratype 2, UF 116701, height 22.4 mm; 6 further specimens (BL. coll.).

Etymology: From its type locality of Cubagua.

Type locality: Cañon de las Calderas, Cubagua Island, Nueva Esparta State, Venezuela.

Type section: Cerro Negro Member, Cubagua Formation, Lower Pliocene.

Diagnosis

A medium sized *Cancellaria* (*Massyla*) with a shell with a relatively depressed spire and strongly inflated last whorl, which is hardly constricted behind the siphonal fasciole, predominant spiral sculpture, strong-

ly developed parietal callus, broad siphonal fasciole and very short siphonal canal.

Description

Protoconch missing. Teleoconch consists of 5.5 convex whorls, with the periphery at the abapical suture. Sculpture on the first two teleoconch whorls worn. Sculpture on the third teleoconch whorl consists of five prominent subequal spiral cords, equal in width to their interspaces, and close-set, strongly prosocline axial lamellae. The number of spiral cords increases abapically, seven on the penultimate whorl, 14–16 on the last whorl, and the axial lamellae become more prominent, about 23 on the last whorl, developing into broad axial folds on the last half whorl. The strength of the axial sculpture is variable, relatively strong in the holotype, giving the last whorl a reticulate appearance, but with the spiral cords predominant, whereas the axial sculpture is much weaker in the paratype. The whole shell surface is covered by very close-set prosocline growth lines. Suture well rounded and deeply impressed. Last whorl strongly inflated, rounded, somewhat barrel-shaped, with the periphery just above mid-whorl, hardly constricted behind the siphonal fasciole. Aperture ovate, outer lip prosocline, thickened by labial varix, strongly and deeply lirate within. Columella straight, with two strong folds, the adapical one much larger, which extends almost to the edge of the thick, well-developed, sharply delimited parietal callus, which is expanded some distance onto the ventral portion on the last whorl, behind which there is a moderately small but deep umbilicus. Siphonal fasciole broad and well developed, bearing six to seven close-set, rounded spiral cords. Siphonal canal extremely short and slightly recurved. The adapical portion of the outer lip bears a strong fold appressed to the body whorl, forming a small anal canal.

Discussion

The Lower Pliocene *Cancellaria* (*Massyla*) *cubaguaensis* nov. sp. is closely related and probably descended from the *C. (M.) cantaurana* Landau and Petit, 1996 from the Lower Miocene Cantaure Formation of Venezuela, but has a larger shell, the spire is squatter, the axial sculpture weaker, the spiral cords stronger, the parietal callus more strongly developed and the siphonal fasciole broader. *Cancellaria* (*Massyla*) *lopezana* Jung and Petit, 1990 from the Lower Miocene, Baitoa Formation of the Dominican Republic is of similar size and also has a low spire, however it differs from *C. (M.) cubaguaensis* nov. sp. in having finer, more numerous spiral cords, the parietal callus is less developed, the siphonal canal is narrower and more elevated, the last whorl constricted behind the fasciole,



Figures 38–48. Figures 38–41. *Cancellaria (Massyla) cubaguaensis* nov. sp. Holotype; MOBR-M-3363 (EDIMAR coll.), Locality 1, Cañon de las Calderas. Height 25.9 mm. Figures 42–44. *Cancellaria (Massyla) cubaguaensis* nov. sp. Paratype, BL coll., Locality 1, Cañon de las Calderas. Height 22.4 mm. Figures 45–46. *Cancellaria (Charcolleria) terryi* Olsson, 1942. BL coll., Locality 1, Cañon de las Calderas. Height 46.0 mm. Figures 47–48. *Trigonostoma (Ventrilia) rucksorum* (Petuch, 1994). BL coll., Locality 1, Cañon de las Calderas. Height 35.9 mm.

and the siphonal canal much longer. *Cancellaria (Massyla) jadisi* Olsson, 1964 from the Upper Miocene Angostura Formation of northwestern Ecuador is also closely similar, with a low spire and a very short siphonal canal, however it differs mainly in the shape of the last whorl, which is more rounded, the periphery at rather than above mid-whorl and more constricted

behind the siphonal fasciole. The holotype of *C. (M.) jadisi* has a parietal callus consisting only of a weak wash as contrasted to the heavy and well-defined callus of *C. (M.) cubaguaensis*. The Floridian Neogene species, such as *C. (M.) venusta* (Tuomey and Holmes, 1856) and *C. (M.) propevenusta* (Mansfield, 1933) all have shells with much longer siphonal canals.

The subgenus *Massyla* H. and A. Adams, 1854 was well represented and diversified in the Caribbean Neogene, but disappeared from the Atlantic during the Pliocene. Two Recent species occur in fairly shallow water in the southern part of the Panamic-Pacific Province, *C. (M.) corrugata* Hinds, 1843 and *C. (M.) obtusa* Deshayes, 1830. There is a third nominal species, *C. (M.) cumingiana* (Petit de la Saussaye, 1844) that is probably a synonym of *C. (M.) obtusa*.

Subgenus *Charcolleria* Olsson, 1942

Cancellaria (Charcolleria) terryi Olsson, 1942

Figures 45–46

Cancellaria (Charcolleria) terryi Olsson, 1942, p. 62, pl. 8, figure 1; Olsson, 1964, p. 124, pl. 22, figure 2; Jung, 1965, p. 556, pl. 75, Figures 17–19; Woodring, 1970, p. 343, pl. 54, Figures 5, 6, 9, 10.

Cancellaria (Charcolleria) sp. - Olsson, 1964, p. 124, pl. 22, figure 1.

Material and dimensions: Single specimen 46.0 mm, Cañon de las Calderas, Cubagua Island (BL coll.).

Discussion

Represented by a single, large, somewhat abraded specimen showing the coarse sculpture characteristic of the species.

Distribution: Atlantic

Lower Miocene: Cantaure Formation, Venezuela (Jung, 1965).

Upper Miocene: Gatun Formation, Panama (Olsson, 1964; Woodring, 1970).

Lower Pliocene: Cubagua Formation, Cubagua Island, Venezuela; Punta Gavilán Formation, Falcón, Venezuela (Woodring, 1970).

Distribution: Pacific

Lower Pliocene: Esmeraldas Formation, Ecuador (Olsson, 1964).

Pliocene (indeterminate): Charco Azul Formation, Burica Peninsula, Costa Rica (Olsson, 1942).

Genus *Trigonostoma* Blainville, 1827

Subgenus *Ventrilia* Jousseaume, 1887

Trigonostoma (Ventrilia) rucksorum (Petuch, 1994)

Figures 47–48

Ventrilia rucksorum Petuch, 1994, p. 351, pl. 88, figure K

Ventrilia kissimmeensis Petuch, 1994, p. 350, pl. 89, figure B

Material and dimensions: Height 36.3 mm. 1 specimen, Cañon de las Calderas, Cubagua Island (BL coll.).

Discussion

A single specimen, in excellent condition, of a *Trigonostoma (Ventrilia)* shell was collected from the Cañon de las Calderas locality. Although this genus had not been recorded from the Lower Pliocene southern Caribbean, other specimens (BL coll.) collected from coeval deposits at Punta Gavilán, on mainland Venezuela, and in the Springvale Formation of Trinidad are almost certainly conspecific with the one from Cubagua. The shell clearly belongs to the *Trigonostoma (Ventrilia) tenerum* (Philippi, 1848) species group. The specimen from Cubagua is characterised by its thin shell, weak sculpture and relatively strongly canaliculated infrasutural platform.

Within the *tenerum* species group Petuch (1994) introduced two new fossil taxa from the Plio-Pleistocene of Florida; *Ventrilia kissimmeensis* and *V. rucksorum*. A single dorsal view of the shell of each of the new species is given, no information on intraspecific variability is presented, and the new taxa are compared only to other new taxa. Neither is compared to *T. (V.) tenerum*, which also occurs in the Florida fossil record.

We have examined specimens of *T. (V.) tenerum* from two Upper Pleistocene, Bermont Formation, localities in Florida, and Pleistocene deposits from Lee Creek Mine in North Carolina. They differ from our shell from Cubagua in having slightly stronger sculpture and a flatter infrasutural platform. We have six specimens (BL coll.) from the Pliocene Pinecrest Beds, from the same locality at the Kissimmee River Canal dig at Okeetantie, Okeechobee County as the shell described by Petuch (1994) as *Ventrilia kissimmeensis*. They are slightly weaker sculptured than *T. (V.) tenerum* and the infrasutural platform is more concave similar to our shell from Cubagua. *Ventrilia rucksorum* described from the Late Pliocene Caloosahatchee Formation is said to differ in having stronger shoulder knobs and having a larger beaded cord around the mid-whorl. If our material from the Kissimmee River is representative of the population, the specimen illustrated as the holotype for *V. kissimmeensis* is unusually smooth and the shell illustrated as *V. rucksorum* is more representative of the species. We provisionally accept *Trigonostoma (Ventrilia) rucksorum* (Petuch, 1994) as distinct, and possibly the predecessor of *T. (V.) tenerum*, and as first revisers (ICNZ, Art. 24.2) choose this name over *V. kissimmeensis*, which we consider an unusually smooth form.

It is not unusual in the Plio/Pleistocene assemblages of Florida to find two congeneric 'species,' occurring

sometimes in the same unit, which are identical except for one consistent difference in sculpture. Vermeij & Vokes (1997) touched on this in their discussion on *Pterorhytis* (*Pterorhytis*) *fluviana* Dall, 1903, and pointed out that specimens found along the Kissimmee River developed elaborately recurved varices (*Pterorhytis lindae* of Petuch, 1994, pl. 10, figure 7). A similar situation can be observed with the presence or absence of axial lamellae in *Eupleura* and *Vokesinotus* species pairs within the same units (Greg Herbert, personal communication 12/07/06 unpublished). This pattern does not seem to be limited to any specific taxonomic group, and probably reflects environmental differences (e.g., wave energy, depth) rather than actual species differences.

Distribution

Lower Pliocene: Cubagua Formation, Cubagua Island, Venezuela.

Plio/Pleistocene: Florida (Petuch, 1994).

CONCLUSIONS

As with previous works dealing with the family Cancellariidae in the Neogene Caribbean faunas (Jung and Petit, 1990; Landau and Petit, 1996), this study shows that, unlike today, a rich and diversified fauna of cancellarids thrived in the Caribbean Pliocene. The number of species known from the Lower Miocene Cantaure formation of Venezuela increases to 14, with the addition of *Cancellaria* (*Bivetiella*) *lugogonzalezorum* nov. sp. and *Cancellaria* (*Bivetopsia*) *herberti* nov. sp., placed in nine subgenus-group taxa. For the Lower Pliocene Cubagua Formation nine species are identified to species-level, plus a group which may contain more than one species, including two new taxa *Cancellaria* (*Cancellaria*) *capeloi* nov. sp. and *Cancellaria* (*Massyla*) *cubaguaensis* nov. sp. These are placed in eight subgenus-group taxa.

The composition of the Neogene southern Caribbean cancellarid fauna is strongly paciphile, with most of the subgenera now restricted to the eastern Pacific. *Bivetiella*, *Bivetopsia*, *Charcolleria*, *Euclia*, *Pyrucilia*, *Massyla* and *Narona*, which are present in the Venezuelan Neogene, all have at least one representative in the Panamic-Pacific faunal province. To this list we can add *Extractrix* Korobkov, 1955, which has been recorded from the Lower Pliocene Punta Gavilán Formation of mainland Venezuela (Jung, 1977). Indeed, of the list of paciphile cancellarid subgenus-level taxa given by Jung and Petit (1990) only *Hertleinia* Marks, 1949, *Sveltia* Jousseau, 1887 and *Perplicaria* Dall, 1890 have yet to be found in the Venezuelan fossil assemblages. The Caribbean cancellarid fauna suffered a severe impoverishment following the uplift of the

Panama Isthmus and closure of the Central American seaway, with only *Cancellaria* (s.s.) and *Cancellaria* (*Ventriolia*) of the larger-shelled taxa present in the Recent faunas.

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Development and Growth of the Hawk Wing Conch, *Strombus Raninus* (Gmelin, 1791) in Culture Conditions: Egg Mass to Early Juvenile Stage

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Abstract. Eight captive-laid egg masses of hawk wing conch, *Strombus raninus*, were used to describe egg mass characteristics, growth rate, and shell morphology of larvae and early juveniles. The egg strand diameter was $357.3 \pm 7.8 \mu\text{m}$; the egg capsule diameter was $129 \pm 7.0 \mu\text{m}$; the number of egg capsules per mm was 19 ± 1.4 ; and the number of eggs per coil of strand was three. Hatching occurred three to four days after the egg mass was laid. The larval shell length at day one was $147.0 \pm 24.0 \mu\text{m}$. The veliger growth rate was $27.4 \mu\text{m}$ per day. The mean size at metamorphosis was $1407 \pm 86.3 \mu\text{m}$, and metamorphic competence occurred at 46 days. Percent metamorphosis using H_2O_2 with a 24 h exposure varied from 16.6% to 52.8%, with a mean of $33.2 \pm 18.3\%$. Post-metamorphic juvenile growth rate was $93.1 \mu\text{m}$ per day. Shell length was $4769 \pm 1235.1 \mu\text{m}$ 36 days after settlement, and shell color was white with brown bands. This data is useful for larval identification from field samples and to aid in culture methodologies.

Key Words: conch, culture, development, growth, larvae, *Strombus*.

INTRODUCTION

In the Caribbean region, there are six conch species belonging to the family Strombidae: *Strombus gigas* Linnaeus (queen conch), *S. costatus* Gmelin (milk conch), *S. raninus* Gmelin (hawk-wing conch), *S. alatus* Gmelin (Florida fighting conch), *S. pugilis* Linnaeus (West Indian fighting conch), and *S. gallus* Linnaeus (rooster-tail conch) (Abbott, 1974). Queen conch, *S. gigas*, is the most commercially fished gastropod in the Caribbean (Randall, 1964; Appeldoorn, 1994). However, populations have been seriously depleted by over-fishing (Stoner, 1997), and the species is now considered commercially threatened (Wells et al., 1983).

Aquaculture has been suggested as a way to replenish natural queen conch populations (Berg, 1976; Brownell, 1977; Ballantine & Appeldoorn, 1983; Davis & Hesse, 1983; Davis, 1994). Methodologies to culture queen conch larvae and juveniles are well established and are used in commercial and research facilities (Creswell, 1984; Corral & Ogawa, 1987; Davis, 1994; Glazer et al., 1997; Davis, 2000; Davis & Shawl, 2005; Davis, 2005). Knowledge of these culturing techniques has allowed researchers to experiment with other *Strombus* species. Research has been conducted to determine growth rates of juvenile *S. costatus* (Berg, 1976; Brownell, 1977; Appeldoorn, 1985), to test phytoplankton diets for *S. gigas*, *S. pugilis*, and *S. costatus* larvae (Aldana-Aranda & Patiño-Suarez,

1998); and to raise juvenile *S. gigas*, *S. costatus*, *S. alatus*, and *S. raninus* in captivity for food production and the aquarium trade (Shawl et al., 2003; Shawl & Davis, 2004).

The larval development of *S. gigas*, *S. costatus* and *S. pugilis* is well known (D'Asaro, 1965; Brownell, 1977; Rodríguez-Gil et al., 1991; Davis, 1994; Brito et al., 2000). However, the information related to *S. raninus* is limited to description of the species, (Clench & Abbott, 1941), distribution (Flores, 1964; Percharde, 1970; Alcolado, 1976; Brownell, 1977), behavior (Berg, 1975), and predation (Arnold & Arnold, 1969; Wodinski, 1969). There are only three studies related to the development or growth of *S. raninus* larvae (Robertson, 1959; Davis et al., 1993; Shawl & Davis, 2004). The main goal of this work was to fully describe the development of the hawk wing conch, *S. raninus*, from egg stage to early juvenile stage in laboratory culture conditions. This information can be used to identify larvae collected in the field, and to aid in the culture of this species.

MATERIALS AND METHODS

The experiment took place from January to March 2002 at Harbor Branch Oceanographic Institution (Harbor Branch), Ft. Pierce, Florida. Egg masses were obtained from captive *S. raninus* adults that were held in the conch facilities at Harbor Branch (Shawl & Davis, 2004). Each egg mass was incubated in an upwelling screen container (15 cm diameter \times 15 cm height) with 50 μm screen on the bottom (Davis, 1994). A continuous flow of re-circulating water (100 ml per

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min per egg mass) passed by the egg strands at a temperature of $26 \pm 3^\circ\text{C}$.

To determine the hatch day, a section of the egg mass strand was observed daily using a dissecting microscope (40 \times). Veligers were ready to hatch when the embryos rotated in the egg capsules. The structures visible prior to hatching were the velar lobes, eye spots, and orange pigments on the foot (propodium). Using a dissecting microscope (40 \times) equipped with an eyepiece micrometer, eight egg masses were used to measure egg strand diameter ($n = 3$ measurements per egg mass), number of eggs/mm of egg strand ($n = 3$ measurements per egg mass), and egg capsule diameter ($n = 5$ measurements per egg mass). The mean and standard deviation were calculated daily for each set of measurements.

When the egg masses were ready to hatch a portion of each egg mass was placed in the bottom of a 4 L bucket that was filled with 10 μm filtered and UV-treated seawater. Culture water was static and aeration was not necessary. Initial larval density was 100–200 veligers per liter (Davis et al., 1993), and the final density in the buckets was 15 veligers per liter. Culture water was changed daily with the aid of a siphon. The veligers were collected on a 100 or 250 μm sieve depending on the developmental stage (Davis, 1994). Larvae were fed Tahitian *Isochrysis* at an initial density of 4000 cells per mL which was increased to 7000 cells per mL over the culture period. The late stage veligers were supplemented with *Chaetoceros gracilis* at 3000 cells per mL of culture water.

After an egg mass hatched, the larvae were observed daily with a dissecting microscope (40 \times). Up to seven egg masses were used to follow larval growth and development. Daily shell length (SL) measurements, apex to siphonal canal, were recorded for ten veligers starting one day after hatch until competence (46 days). The number of velar lobes, number of shell whorls, foot development, shell beak, and foot pigmentation was described. As larvae approached metamorphic competence, features such as the presence of ctenidium, foot pigmentation, and eye migration were recorded. Scanning electronic microscopy (SEM) photos of larval shells were taken at every 15 days of development (1, 15, 30 and 45 days old), using a Scanning Electronic Microscope Topcon, Model SM-510 from El Colegio de la Frontera Sur (ECOSUR)-Tapachula, Mexico.

Metamorphosis was induced using 3% hydrogen peroxide (0.06 ml H_2O_2 per L seawater) (Boettcher et al., 1997; Davis & Shawl, 2005). To determine metamorphic success, three replicates of 20 animals each were placed into individual 4 L buckets. After four hours of exposure to the H_2O_2 inducer, the number of larvae swimming, metamorphosed, or dead was counted. The larvae were then placed back into the buckets with the H_2O_2 inducer, and were counted again 24 h later. Shell length of newly settled juveniles was

Table 1

Daily egg mass characteristics of *S. raninus* before hatch. The results are expressed as mean \pm standard deviation (n = no. egg masses).

Variable	Diameter of egg strand (μm)	No. egg capsules per mm	Egg capsule diameter (μm)
Day 1 ($n = 8$)	357 ± 7.8	19 ± 1.4	129 ± 7.0
Day 2 ($n = 7$)	351 ± 6.2	19 ± 1.2	131 ± 7.8
Day 3 ($n = 6$)	381 ± 12.1	20 ± 1.7	137 ± 8.9
Day 4 ($n = 4$)	377 ± 7.2	21 ± 1.7	133 ± 1.0

measured weekly for 36 days and morphological changes were observed daily.

RESULTS

The egg strand dia, egg capsule dia, and the number of egg capsules per mm were measured for eight *S. raninus* egg masses (Table 1, Table 2). The diameter of the egg strand increased by 20 μm from the spawning day ($357 \pm 7.8 \mu\text{m}$) to one day before hatching ($377 \pm 7.2 \mu\text{m}$). The dia of the egg capsule increased from $129 \pm 7.0 \mu\text{m}$ at day one to $133 \pm 1.0 \mu\text{m}$ by day four (Table 1). The mean number of egg capsules per mm was 19 ± 1.4 ($n = 8$) (Table 1). The number of eggs per coil of strand was three (Table 2). Eggs hatched in four days at a mean incubating temperature of 26.3°C .

At hatch, the larvae were active and showed positive phototaxis. Newly hatched veligers were $147.0 \pm 21 \mu\text{m}$ SL ($n = 5$ egg masses) (Figure 1), had two rounded velar lobes (125 μm in length), and a shell with one and a quarter whorls (Figure 2A, B). At metamorphic competence, veliger SL was 1407 μm ($n = 1$ egg mass), they had six elongated lobes (3000 μm), and the shell had five whorls (Figure 2G, H). Description of larval development is described in Table 3. The growth curve showed a sigmoid shape: a fast growth rate was observed at early stage (until day 30) and decreased as the larvae became competent (Figure 1). The overall growth rate was 27.4 μm per day ($n = 111$ veligers).

On day 1, the SEM showed that the larval shell has one and a quarter whorls and a small beak (Figure 2). It is elliptical and lightly flat, and the siphonal length was $147 \pm 21 \mu\text{m}$ ($n = 5$ egg masses) (Figure 2A, B, Table 2, 3). By day 15, the shell has three and a half whorls and a shell length of $599 \pm 211 \mu\text{m}$ ($n = 2$ egg masses). The first whorl at the top is the protoconch, and the second whorl is located at the center in the columnella axis. The third whorl is twice the size of the second whorl and shows the beakline, which is comprised of three bands (Figure 2C, D, Table 3). The shell has four and a half whorls and a shell length

Table 2

Summary of egg mass and veliger characteristics of *S. raninus*. The results are expressed as mean \pm standard deviation (n = no. egg masses).

Variable	Robertson, 1959	Davis et al., 1993	Shawl and Davis, 2004	This study
Diameter of egg strand (μm)	—	321 ± 20 (10)	351 ± 24 (40)	357 ± 7.8 (8)
No. egg capsules per mm	20–23 (1)	21–25 (15)	15–34 (40)	19–21 (8)
Egg capsule diameter (μm)	140 ± 4 (30)	—	123 ± 10 (40)	129 ± 7.0 (8)
No. eggs per coil	—	3	—	3
No. eggs/mass	400,000–460,000	206,000–245,000	91,000–250,000	180,000*
New hatched veliger SL (μm)	—	197 ± 8 (20)	205 ± 10.5 (10)	147 ± 21.0 (5)
Size at competence (μm)	—	1450 ± 53 (10)	1438 ± 72.2 (4)	1407 (1)

* Calculated based on 9 m strand length and an average of 20 egg capsules per mm (Shawl & Davis, 2004).

of 1080 μm (n = 1 egg mass) at age 30 d. Several fine transverse lines are apparent. The last whorl shows the beakline, which appears to have markings in the shape of a “C” (Figure 2E, F, Table 3). Near competency (day 45), the shell has five whorls and a shell length of 1407 μm (n = 1 egg mass). Transverse lines are more noticeable on each whorl, and the beakline is apparent (Figure 2G, H, Table 3).

Towards the end of the larval cycle, the veligers showed a swim-crawl behavior and stayed near the bottom of the culture vessel. The foot, adult operculum, and gills were fully developed at competence. Metamorphosis was induced when ctenidium were observed in 90% of the larvae (38–46 days old). During metamorphosis the lobes were absorbed, the larval heart became non-functional, and the proboscis was developed. The percentage of larvae that completed metamorphosis after four hours was $0.6 \pm 0.9\%$ (n = 3 replicates of 20 veligers). When the veligers were

reinduced for an additional 24 hr, the percentage of metamorphosis increased to $33.2 \pm 18.3\%$ (n = 3 replicates of 20 veligers).

During the first days after metamorphosis the shell was amber in color, and some internal structures could be observed through the shell. There were several longitudinal lines on the shell along with transverse lines. By day 10, small squares were visible on the shell, and the thickness of the shell increased and was no longer transparent. The eyes began to migrate up the eyestalks two days after metamorphosis, but the migration to the top of the stalk was not complete until 30 d after metamorphosis, when the length of the eyestalk was 575 μm and the tentacle length was 750 μm . At 36 d after metamorphosis, the shell was white with brown bands and was 4767 ± 1235.1 μm (n = 29 juveniles) in length. The mean growth rate of the metamorphosed juveniles was 93.1 μm per day (n = 90 juveniles) (Figure 3).

DISCUSSION

Veligers in the family Strombidae have varying larval development. After internal fertilization, the female deposits a gelatinous sand covered egg mass on the substrate. Within the egg mass capsules, the embryos develop to trochophore stage. When development is complete, larvae hatch as veligers and become members of the plankton (Young, 2001).

The egg strand diameter is variable between *Strombus* species. Measurements from egg masses collected in captivity show that the larger species, *S. gigas* & *S. costatus*, have the widest strand diameter, 798 ± 18 μm and 825 ± 56 μm , respectively (Shawl & Davis, 2004). *S. alatus* has a strand diameter of 509 ± 41 μm and *S. raninus* has the smallest diameter, 351 ± 24 μm (Shawl & Davis, 2004). Robertson (1959) observed similar measurements for egg masses collected from the wild in the Bahamas. In this study the egg strand diameter for *S. raninus* (357 ± 7.8 μm) was slightly wider than reported by Shawl & Davis (2004).

The egg capsule diameter measured in this work (129

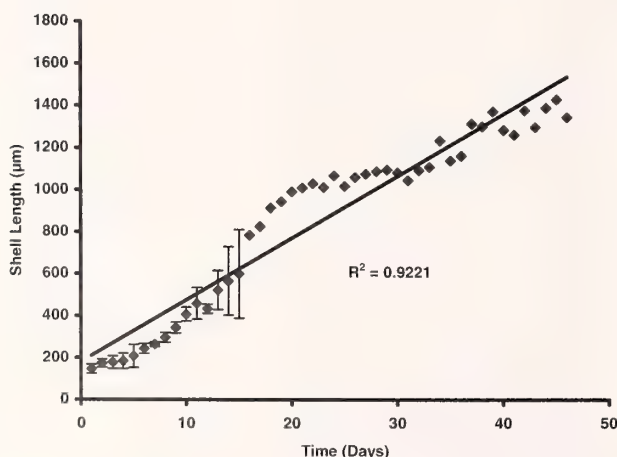


Figure 1. Growth curve of *S. raninus* larvae in laboratory conditions over the experimental period (January–March 2003). Results are expressed as mean \pm standard deviation (day 1, n = 5 egg masses; day 2–5, n = 6 egg masses; day 6–8, n = 4 egg masses; day 9–11, n = 3 egg masses; day 12–15, n = 2 egg masses; day 16–46, n = 1 egg mass).

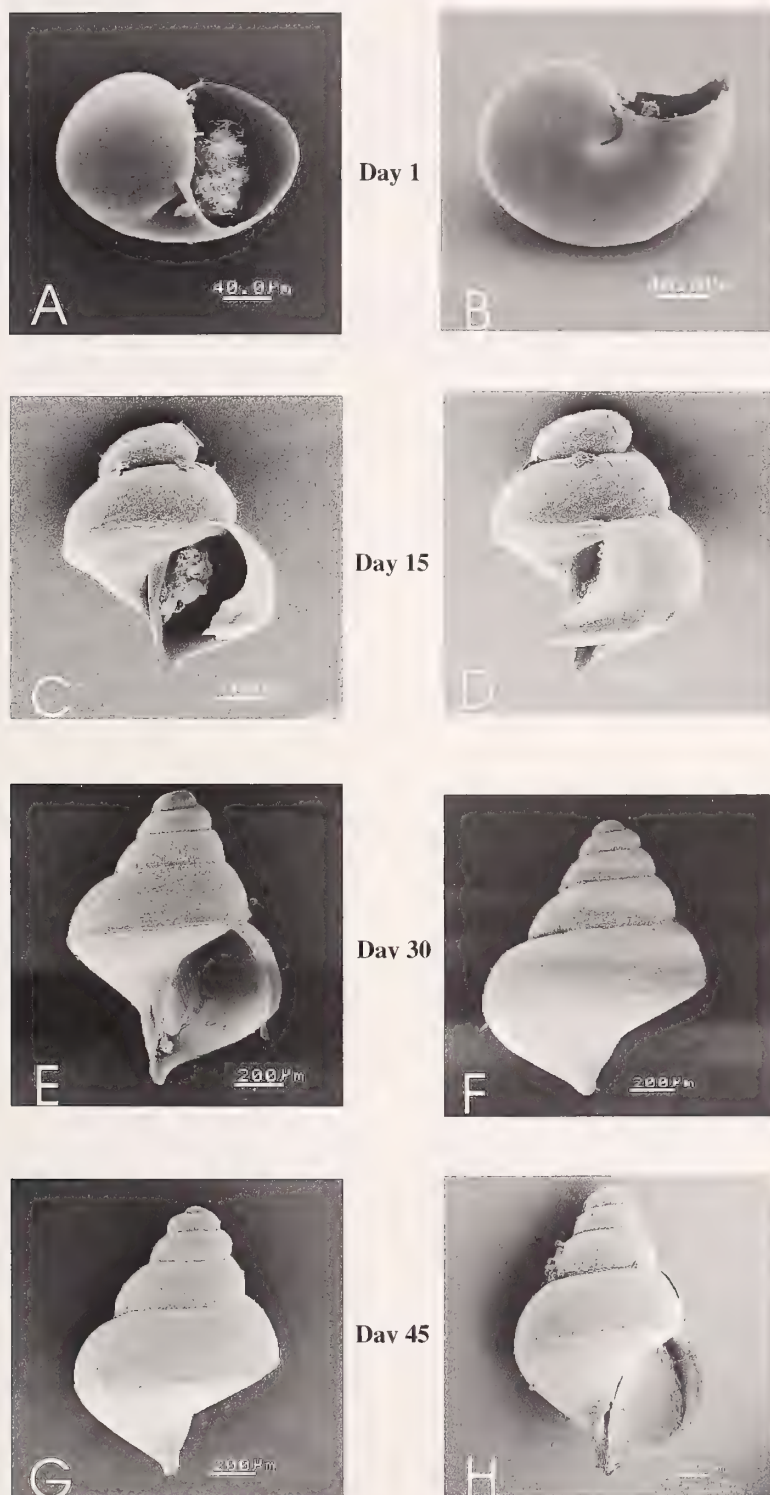


Figure 2. SEM photographs of *S. raninus* larvae. Scale bar in μm .

Table 3
Description of *S. raninus* veliger development.

Days	Development description
1	Larvae are extremely active and show a positive phototaxis. The shell is transparent with 1 ¼ whorls, a small beak, and it is elliptical and slightly flat. Two round lobes are visible (125 µm), and larvae select food particles. Retinal cells are on the cerebral area (Fig. 2A, B).
2–4	The shell has 1 ½ whorls. The shell beak has elongated. Larval and adult hearts are visible. Lobes are expanded (150 µm diameter). Food is obvious in the digestive glands, and the crystalline style rotates in the stomach.
5–6	Veligers have two lobes. In the middle of the each velar lobe there is an indentation to form four lobes (200 µm dia). Shell has two whorls and the beak is elongated. Orange pigment is observed on the foot.
7–8	The shell has 2 ½ whorls and shows an elongated beak. Veligers have two large lobes (350 µm dia) with a larger indentation. The right tentacle is formed.
9–10	Shell has three whorls, and beak is well developed. Lobes continue their indentation to four lobes.
11–12	The shell has 3 ½ whorls. The veliger has four lobes (500 µm dia).
13–14	The shell has 3 ½ whorls with an elongated beak (Fig. 2C, D). The first whorl at the top is the protobranch, and the second whorl is located at the center in the columnella axis. The third whorl is twice the size of the second whorl and shows the beakline, which is comprised of three bands. Dorsal lobes begin to divide into six lobes.
15–17	Six lobes are complete. The propodium is more developed and active. There are orange pigments on the propodium, metapodium, and mantle.
18–22	The shell has four whorls and six elongated lobes (600 µm dia). Left tentacle is half the size of right tentacle.
22–25	The six lobes have increased in length (800 µm dia).
25–27	Stomach and digestive gland well developed. Crystalline style rotates actively. Tentacles are still unequal in length. Osphradium is visible.
28–30	Six lobes are well developed (1400 µm dia). The shell has 4 ¼ whorls (Fig. 2E, F). Several fine transversal lines are apparent. The last whorl shows the beakline, which appears to have markings in the shape of a “C”. Ctenidium starts to develop. Eyes are at the base of the stalks. Statocyst visible as two bright dots.
31–33	Shell has 4 ½ whorls. The propodium is active.
34–37	Metapodium is constricted and thinner.
38–41	Ctenidium is present, foot is active and veliger shows swim-crawl behavior.
42–45	The shell has five whorls (Fig. 2G, H). Transverse lines are more noticeable on each whorl, and the beakline is apparent. Ctenidium is fully developed and present in 100% of larvae. Six long lobes (3000 µm dia). Operculum has a claw.

$\pm 7.0 \mu\text{m}$), was larger than that observed by Shawl & Davis (2004) ($123 \pm 10 \mu\text{m}$), but it was smaller than that reported by Robertson (1959) ($140 \pm 4 \mu\text{m}$). The number of eggs per mass for *S. raninus* reported by Robertson (1959) ranged from 400,000 to 460,000. Davis et al. (1993) found that the number of eggs per mass ranged from 206,000 to 245,000, and Shawl & Davis (2004) recorded the number of eggs per mass varied from 91,000 to 250,000. In this work the number of eggs per mass was estimated to be 180,000 based on an average egg strand length of 9 m (Shawl & Davis, 2004) and 20 egg capsules per mm (this study).

The veligers from the egg masses in this study hatched in 80 hr, which coincided with the time observed by Robertson (1959). The morphological features and development of *S. raninus* are similar to other *Strombus* species, such as *S. gigas*, *S. costatus* and *S. pugilis* (D'Asaro, 1965; Davis, 1994; Brito et al., 1999). However, growth rate was slower and time to

metamorphosis was longer compared to some other *Strombus* species. In this study a larval growth rate of $27.4 \mu\text{m}$ per day was calculated for *S. raninus*, which is lower than *S. gigas*, ($39 \mu\text{m}$ per day), *S. costatus* ($31 \mu\text{m}$ per day) (Davis et al., 1993), and similar to *S. pugilis* (25 to $27 \mu\text{m}$ per day) (Brito et al., 2000). Compared to other *Strombus* species, the hawk wing conch had the longest development time to metamorphosis (46 days). These are similar results from Davis et al. (1993) and Shawl & Davis (2004); they found time to metamorphosis for *S. raninus* to be 40 days and 48 days, respectively. Average development time is 28 days for *S. costatus*, 21 days for *S. gigas*, 31 for *S. pugilis*, and 24 days for *S. alatus* (Davis et al., 1993; Brito et al., 2000; Shawl & Davis, 2004). *S. raninus* have a slightly larger shell length at metamorphosis ($1407 \pm 86 \mu\text{m}$) compared to *S. costatus* ($1306 \pm 23.9 \mu\text{m}$), *S. gigas* ($1282 \pm 63 \mu\text{m}$), *S. pugilis* ($1022 \mu\text{m}$), and a smaller shell length than *S. alatus*

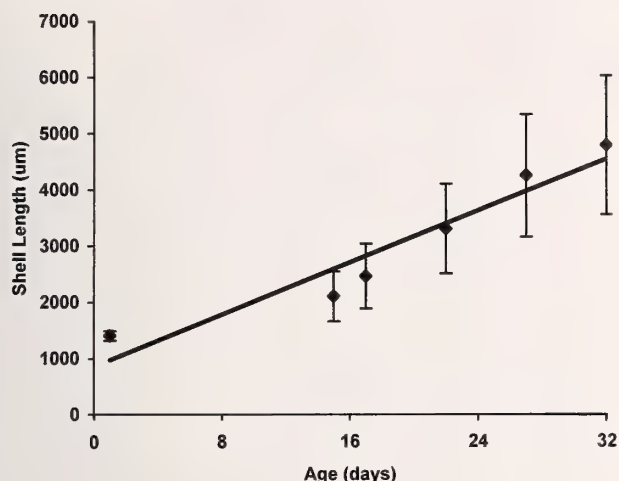


Figure 3. Growth of juvenile *S. raninus* for 36 days following metamorphosis. Results are expressed as mean \pm standard deviation (day 1, $n = 61$ juveniles; day 15, $n = 5$ juveniles; day 17, $n = 35$ juveniles; day 22, $n = 34$ juveniles; day 27, $n = 30$ juveniles; days 32 and 36, $n = 29$ juveniles).

($1539 \pm 186 \mu\text{m}$) (Davis et al., 1993; Brito et al., 2000; Shawl & Davis, 2004).

Shawl & Davis (2004) demonstrated that *S. raninus* could be induced to undergo metamorphosis with low concentrations of hydrogen peroxide; however, percent metamorphosis was low ($5.3 \pm 2.3\%$) after four hours of exposure. In this study, $0.6\% \pm 0.97$ of the veligers completed metamorphosis with the same exposure time (4 h). However, there was a substantial increase in metamorphosis when the larvae were exposed to the inducer at the same concentration for 24 hr ($33.2 \pm 18.28\%$). Juvenile growth rate (post-metamorphosis) of *S. raninus* had not been previously recorded, and the rate of $93.1 \mu\text{m}$ per day is slightly lower than the average *S. gigas* growth rate range of $180\text{--}250 \mu\text{m}$ per day.

The hawk wing conch differ from the other *Strombus* species in the larval phase, shell size at metamorphosis, and growth rate. *S. raninus* adults have shown a higher fecundity (Shawl & Davis, 2004) in captivity, compared to other *Strombus* species (*S. alatus*, *S. costatus*, and *S. gigas*). However, their small size at hatch, the long development time, and the low metamorphic success rate does not make *S. raninus* a prime candidate for aquaculture. In natural populations, the extended larval cycle may represent a long residence in the plankton and it could permit a wider dispersion of *S. raninus* larvae in the Caribbean (Davis et al., 1993). This could be due to an inter-specific difference in colonizing new environments, and to diminish competition between *Strombus* species.

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Instructions to Authors

The Veliger publishes original papers on any aspect of malacology. All authors bear full responsibility for the accuracy and originality of their papers.

Presentation

Papers should include an abstract (approximately 5% of the length of the manuscript), Introduction, Materials and Methods, Results, and Discussion. Short notes should include a one-sentence abstract. In taxonomic papers, all names of taxa must be accompanied by author and date of publication, and by a full citation in the bibliography. In papers on other subjects and in the non-taxonomic portions of taxonomic papers, author and date of names need not be accompanied by a full citation. All genus and species names should be in italics. All references to new molecular sequences must be linked to GenBank.

Literature Cited

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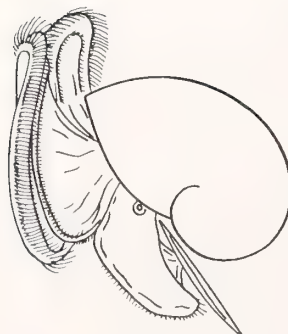
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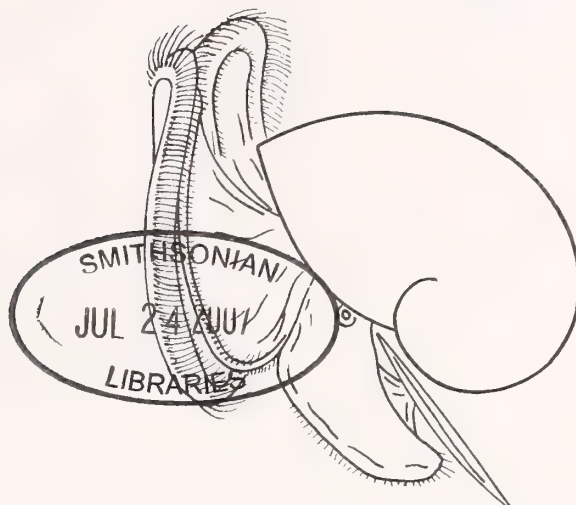
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Aesthete Canal Morphology in Twelve Species of Chiton (Polyplacophora)

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Abstract. Epoxy casts were made of the aesthete canal system in chiton valves (shell plates) from twelve species, representing four families and the three major modern suborders of the Polyplacophora. In this study, Mopaliidae was represented by *Mopalia muscosa*, *Mopalia acuta*, *Nuttallochiton hyadesi*, and *Placiphorella velata*; Tonicellidae by *Lepidochitona hartwegii* and *Nuttallina californica*; Ischnochitonidae by *Lepidozona cooperi*, *Lepidozona mertensii*, *Lepidozona pectinulata*, *Ischnochiton textilis*, and *Ischnochiton variegatus*; and Lepidopleuridae by *Lepidopleurus cajetanus*. The casts reveal a diversity of large and small-scale canal forms in the chitons studied. However, members of each suborder and family share fundamental features of the aesthete canal system, which suggests that epoxy casting of the aesthete canals provides a set of characters useful in future taxonomic and phylogenetic studies of chitons. The casts also reveal a greater connectivity in the total aesthete canal system than is widely realized. For instance, canals in the apical area connect to those in the slit rays, the ventral area below the jugum, and the dorsal surface of the valve. Canal morphology also seems to be influenced by the shell layer in which canals occur. For example, those canals that exist within the articulamentum are much more flattened in cross section than those that occur in the tegmentum.

INTRODUCTION

Chiton valves (shell plates) consist of a thin outermost organic periostracum layer and three underlying aragonitic layers: tegmentum (upper), articulamentum (middle), and hypostracum (lowermost). The principal shell layers are the tegmentum, which bears the shell sculpture, and the underlying denser articulamentum, whose marginal projections form the insertion plates and sutural laminae (Baxter & Jones, 1981). Marshall (1869) was the first to describe the tissue-filled canal system that penetrates the chiton tegmentum, pointing out that fine vertical canals at the surface connect to bulbous cavities that in turn lead to horizontal canals that run at the interface between the tegmentum and articulamentum. The tegmentum is penetrated by

canals through much of its volume, and the distribution and nature of the canal elements varies between the valve areas in at least some chitons (Fischer & Renner, 1979). Although most discussion of aesthete canals in chitons has focused on the tegmentum layer where the canals are densest, the presence of pores in the jugal sinus and slit ray regions of the ventral surface of the valves indicates that the aesthete canal system infiltrates the articulamentum layer in certain areas (Baxter & Jones, 1981).

Moseley (1884, 1885) was one of the first to describe aesthete tissues in fine histological detail, noting the occurrence of two distinct size classes: he named the larger ones megalaesthetes and the smaller ones microaesthetes. In addition, he discovered “eyes,” or ocelli, characterized by a refractive lens and the presence of pigmentous cells seen in much larger chambers within the valves of certain chiton species (Moseley, 1885), and Boyle (1969) nearly a century later confirmed the presence of photoreceptors within these “eyes.”

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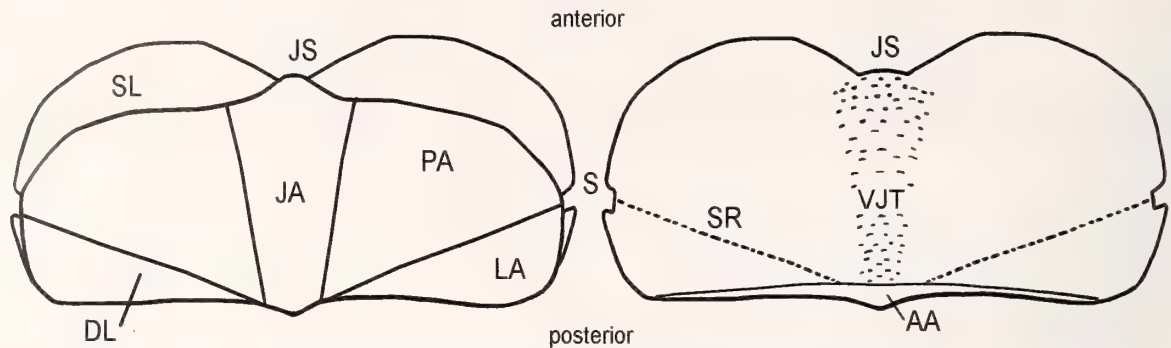


Figure 1. Drawing of chiton valve showing terminology (dorsal valve surface on left; ventral on right). Key: JS = jugal sinus; SL = sutural laminae; DL = diagonal line; S = slit; SR = slit ray; JA = jugal area; PA = pleural area; LA = lateral area; AA = apical area; VJT = ventral jugal triangle.

Micraesthetes typically consist of a single cell with its nucleus lodged within the megalaesthete chamber. Megalaesthetes are larger, multicellular organs generally composed of several secretory cells, microvillous cells (central cells), one or more photoreceptor cells, and peripheral cells (Fischer, 1988; Eernisse & Reynolds, 1994). However, megalaesthete cellular composition varies between species and at least one species, *Tonicella marmorea*, lacks photoreceptor cells altogether (Baxter et al., 1987). Ocelli, which occur in much larger spaces that are thought to be modified megalaesthete chambers, have so far been found in just a few chiton species and are sparsely distributed on the valve surface in those species (Moseley, 1885; Boyle, 1969; Boyle, 1976).

The function of the typical (non-ocelli) aesthetes been debated, with proposals including chemoreception (Fischer, 1988); mechanoreception (Moseley, 1885); periostracum replenishment and secretion (Boyle, 1974; Baxter et al., 1990); secretions serving protective functions (Fischer, 1988); and photoreception (Moseley, 1885; Blumrich, 1891; Omelich, 1967; Boyle, 1972; Fischer, 1978, 1988). An early electron microscopy study (Omelich, 1967) and a more recent immunocytochemical study (Reindl et al., 1997) have shown that aesthetes clearly contain neuronal structures, suggesting a sensory function. The presence of photoreceptive cells and ocelli in larger aesthete complexes, along with the fact that many chitons have been shown to be positively or negatively phototactic (e.g., Crozier, 1920; Omelich, 1967; Boyle, 1972; Fischer, 1988; Currie, 1989), has led many to view photoreception as one of the primary functions of aesthetes, although it seems likely that aesthetes serve multiple roles (Haas and Kristen, 1978; Fischer, 1979, 1988).

Baxter & Jones (1981, 1984) described three main types of aesthete canal (channel) systems that occur in distinct areas of the valves of *Lepidochitona cinereus* and *Callochiton achatinus*: multiple branch channels, found in the lateral and pleural areas (see Figure 1 for an illustration of chiton valve terminology); jugal area

channels; and slit ray channels. Multiple branch channels open along the anterior margin of the tegmentum. These branch repeatedly along their horizontal pathway through the tegmentum, with branches subsequently leading up to megalaesthete and micraesthete canals just below the valve surface. Slit ray channels open along the lines of pores (slit ray) on the ventral surface of valves that have slits in the insertion plates, as occurs in most chiton species. Baxter and Jones (1981) argued that these channels pass dorsally and posteriorly from the ventral openings through all shell layers to open at the dorsal valve surface. Jugal area channels form a triangular area of pores on the ventral valve surface and are similar to slit ray channels because they were also thought to pass through all valve areas to open on the dorsal surface (Baxter and Jones, 1981).

Moseley (1885) proposed that the structure and arrangement of the "eyes" in those chitons that have them could be useful in phylogeny. More broadly, Leloup (e.g., 1934, 1936, 1937, 1940a, 1940b, 1942, 1948, 1952) incorporated many drawings of the patterns of micraesthetes and megalaesthete chambers in his taxonomic descriptions of numerous chiton species. More recent workers (e.g., Boyle, 1974; Baxter & Jones, 1981, 1984; Baxter et al., 1987; Fischer, 1988; Currie, 1989; Baxter et al., 1990; Currie, 1992; Sturrock & Baxter, 1993; Reindl et al., 1997) have also documented aesthete and aesthete canal morphology in different chiton species. These studies have shown that the fine scale form of the aesthetes and the canals that house them vary between species and so represent characters that could be used in phylogenetic analyses. In fact, aesthete pore densities and arrangements on the valve surface have already been used in phylogenetic studies (e.g., O'Neill, 1985; Bullock, 1985). However, it still seems true that, as Currie (1992:3) wrote, "The paucity of information on aesthete morphology and distribution in a range of chiton species/families, and indeed habitats, clearly remains a hindrance to our understanding of aesthete function and evolution."

Epoxy casts have been used to infer the shape of tunnels in shells with endolith borings (e.g., Golubic et al., 1970; Vogel & Marincovich, 2004) and shell pores in limpets (Reindl and Haszprunar, 1994). In addition, Haas & Kriesten (1978) used this method to obtain details of the aesthete canal system in *Chiton albolineatus*, revealing short micraesthete canals that feed into elongate megal aesthete chambers that connect to a small number of large horizontal canals. Vendrasco et al. (2004) used the epoxy casts of a chiton valve to compare with the tunnels in valves of multiplacophorans, an unusual type of Paleozoic chiton.

The purpose of this study was to provide more information about: (1) the morphology of the total aesthete canal system; (2) how aesthete canal patterns differ between a set of chiton species; and (3) whether aesthete canal patterns correlate best with taxonomic relationships or environmental factors.

MATERIALS AND METHODS

Individuals of *Mopalia muscosa* (Gould, 1846) (Santa Barbara Museum of Natural History (SBMNH) 83143 and 83144), *Lepidochitona hartwegii* (Carpenter, 1855) (SBMNH 83146 and 83147), and *Nuttallina californica* (southern form; previously *Nuttallina fluxa*) (SBMNH 83148–83149) were collected by CZF and MJV in the middle to lower intertidal of Palos Verdes, California on the surface of rocks. Individuals of *Lepidozona pectinulata* (Carpenter in Pilsbry, 1893) (SBMNH 83152 and 83153) were also collected from Palos Verdes, from under submerged stones in the lower intertidal. Individuals of *Lepidozona cooperi* (Dall, 1879) (SBMNH 83150 and 83151), one specimen of *Nuttallina californica* (Nuttall MS, Reeve, 1847) (SBMNH 83156), and one specimen of *Lepidozona mertensii* (von Middendorff, 1847) (SBMNH 83145) were collected by MJV from the rocky intertidal of Cambria, California. Specimens of *Mopalia acuta*, *Placiphorella velata*, *Lepidozona mertensii*, *Ischnochiton textilis*, and *Ischnochiton variegatus* were obtained from the SBMNH and isolated valves of *Nuttallochiton hyadesi* were provided by the Los Angeles County Museum (LACM). All other chitons were obtained from shell dealers.

One specimen of *Ischnochiton textilis* (Gray, 1828) (SBMNH 83158) was collected from intertidal rocks in Chelsea Point, Port Elizabeth in the Eastern Cape, South Africa; the other (SBMNH 369435) is from the George Hanselman collection, also collected from Port Elizabeth, South Africa at 0–2 m. One specimen of *Ischnochiton variegatus* (H. Adams and Angas, 1864) (SBMNH 83159) was collected under rocks in the intertidal zone in DeMole Point, South Australia; the other (SBMNH 369437) was collected from Port MacDonnell in South Australia, under small rocks

with sand in the intertidal. One individual of *Mopalia acuta* (Carpenter, 1855) (SBMNH 83160) was collected half buried in sand on the side of a rock in Doheny Beach, Orange County, California; the other (SBMNH 369432) was collected from Oceanside, near Camp Pendleton, on cobble reef on the underside of a rock in the intertidal zone during a -0.37 m tide. One individual of *Placiphorella velata* Carpenter MS, Dall, 1879 (SBMNH 83161) was collected from the intertidal zone in Pacific Grove, Monterey Peninsula, California; the other (SBMNH 369440) is from the Spencer Thorpe collection, found in Timber Cove, Sonoma County, California on a rock in the intertidal zone. *Nuttallochiton hyadesi* (de Rochebrune, 1889) (SBMNH 83157) had been dredged from a depth of 384–494 m at $56^{\circ}06'S$, $66^{\circ}19'W$ off the coast of Tierra del Fuego. One specimen of *Lepidozona mertensii* (SBMNH 369438) was collected from Port Gamble, Washington, USA in the intertidal. One specimen of *Lepidopleurus cajetanus* (SBMNH 83154) was collected at 2.5–4 m depth under stones in Galeria, Corsica, Mediterranean; the other individual (SBMNH 83155) on the coast of Croatia under rocks on sand in the lower intertidal. All chitons used in this analysis were adults.

Valves from at least two individuals from each species were used, except for the rare *Nuttallochiton hyadesi*. Both the northern and southern form (the latter was previously named *Nuttallina fluxa*) of *Nuttallina californica* were used. Valves from only one individual of the northern form was examined, although two individuals of the southern form were processed. One to three intermediate valves of each individual were embedded and examined.

Whole specimens were boiled so the valves could be removed from the flesh. Even isolated shell plates were boiled in order to clean them. The isolated intermediate valves of all species were soaked in bleach for up to 24 hr and placed in a sonicating bath for 25 min at room temperature to dislodge remnant organic material and other debris. Valves were dehydrated through an ethanol series and then embedded in epoxy using a method modeled after (Golubic et al., 1970). A low viscosity embedding medium was created using the Embed 812 kit from Electron Microscopy Sciences. The Embed 812 kit consisted of Embed 812 embedding resin, Dodecenyl Succinic Anhydride (DDSA), Nadic Methyl Anhydride (NMA), and Benzyldimethylamine (BDMA). They were combined in the following proportions: 44.1% Embed 812, 35.3% DDSA, 17.6% NMA, and 2.9% BDMA. The valves were submerged in resin and placed under a vacuum in a desiccating chamber for 24 hr and then cured in an oven at $60^{\circ}C$ for 24 hr. The cured blocks were trimmed using a Buehler low speed saw or with a dremel tool using a thin-bladed saw. Cuts were made around the edges of the valves, making sure to intersect the valve on all

sides. The blocks were placed in 10% HCl for another 24 hr or until all of the calcium carbonate dissolved away, then rinsed with distilled water, cleaned with bleach, and split apart into a dorsal and ventral cast. The resultant casts were gold sputtered and most were examined under SEM using a LEO 1430 with an accelerating voltage of 10–15 kV.

The cladistic analysis using aesthete characters was performed using PAUP 4.0b10 (Swofford, 2002). An exhaustive search was completed using maximum parsimony; all characters were unweighted and all character states were unordered.

Assignments to chiton orders and families were based on Sirenko (1997), although alternative taxonomic schemes are mentioned in the Discussion of this paper.

Isolated valves and epoxy casts of each species in the analysis were deposited in the chiton collections of the Santa Barbara Museum of Natural History.

RESULTS

In this section, the trend of the canal system is described in a manner consistent with the direction of valve growth (see Baxter & Jones, 1981, 1984) and the flow of sensory information. The openings of the canals on the dorsal surface of the valve are taken to be the origin and the places where the canals enter the body of the chiton (e.g., at the anterior and lateral eaves) are described as the exit. The portions of the valve surface referred to in the text are shown in Figure 1. All directional indicators (anterior, posterior, dorsal, ventral) are meant with respect to the valve in life position. The two pieces of the aesthete canal cast are referred to as dorsal and ventral, also defined based on life position.

Lepidopleurus cajetanus (Lepidopleurina: Lepidopleuridae)

The dorsal casts (Figures 5f–h) reveal micraesthetes (~4–6 μm diameter) that feed into a bulbous megal aesthete chamber (~30–60 μm diameter), that then connects to a single, narrow (~10 μm diameter) horizontal canal that leads to the anterior or lateral margin. Megalaesthetes are arranged in anterior-posterior rows along the ridges of the central area. The megal aesthetes are much denser, and less organized, in the ridged lateral areas. The megal aesthete bulbs typically have a sub-cylindrical shape in the central area, often with a constriction at the base where they attach to, or become, the horizontal canal. In some cases the bulbs have a more expanded tent-like shape and have a greater number of micraesthetes (>10 vs. ~7) feeding into them. There is a distinct spacing of ~10 μm between adjacent aesthete complexes in the central area, leading to a clustered appearance of

aesthete pores on the dorsal valve surface. The canals have a meandering, somewhat interweaving pathway from megal aesthete bulb to valve margin.

The ventral casts show that a large number of aesthete canals terminate on the ventral surface of the shell plate, even though *Lepidopleurus* lacks the slit rays and associated ventral slit ray canals. There is an abundance of canals in the ventral jugal triangle, at and near the apical area, and in the region underneath the lateral areas.

Mopalia muscosa (Acanthochitonina: Mopaliidae)

The dorsal casts (Figures 2a–c) reveal nearly straight, primary horizontal canals (~20–35 μm in diameter) that run from the posterior to the anterior margin through all valve areas. The canals are closely spaced (~12–20 μm between primary canals; ~20 canals per mm along the horizontal plane) and in some cases adjacent horizontal canals merge with each other. At least two layers of primary horizontal canals can be seen as they near the anterior margin of the valve. There are also many smaller-diameter (~10–20 μm), short, connecting canals, above and sub-parallel to primary horizontal canals, that merge with the primary canals at regular intervals. The connecting canals, and in some instances the primary horizontal canals, connect to the dorsal valve surface via a megal aesthete chamber fed into by a megal aesthete or micraesthete canal. Micraesthete canals are ~2–3 μm in diameter. Megalaesthete canals begin as a short length of canal with a diameter of ~6–7 μm , before gently flaring out to a diameter of ~15–25 μm as they continue down towards the horizontal canals. At the top of the casts of the micraesthete canals and megal aesthete chambers are cup-shaped protuberances that appear to be filled-in subsidiary (~6–8 μm diameter) and apical (~10–11 μm) caps, respectively.

In the jugal area, some horizontal canals have a more flattened appearance and turn down towards the ventral valve surface. On the ventral casts (Figures 2d–f), the corresponding area (herein referred to as the ventral jugal triangle) has short lengths of similarly flattened canals. These ventral canals occur along valve growth lines; ~2–5 canals per growth line can be seen on the cast. A number of canals pass from the apical area into the ventral jugal triangle.

Some canals (visible on the dorsal casts) near the boundary of the pleural and lateral areas, along the diagonal line, are turned downwards. The canals in this region originate dorsally and merge with each other (on average, 2–3 canals merge) as they near the ventral valve surface. On the ventral cast, a single line of horizontal canals is present parallel to the slit ray; on *Mopalia muscosa* valves, slit rays correspond exactly to the diagonal line.

The ventral casts show the apical area canal system

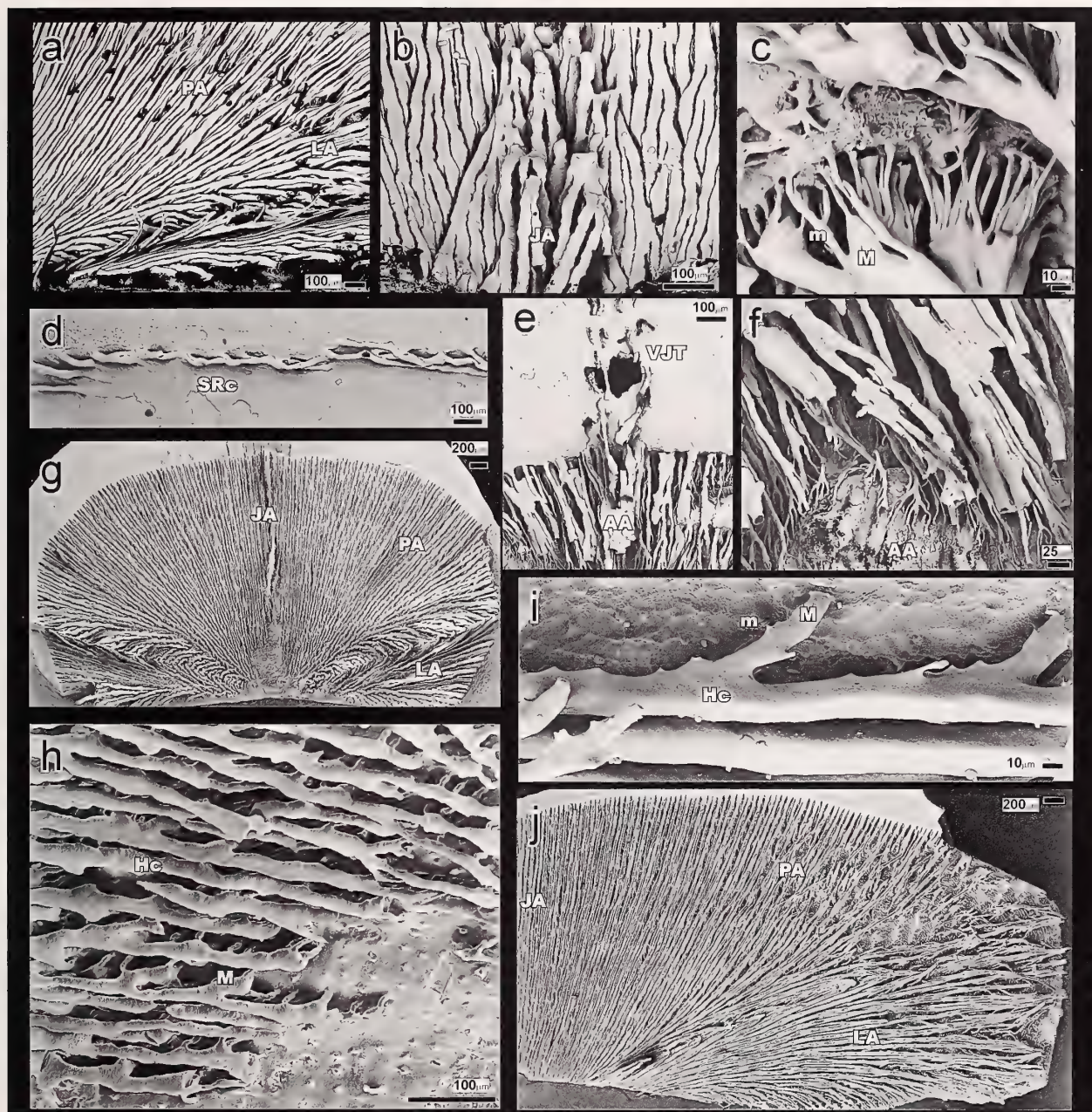


Figure 2. SEM images of casts of aesthete canal systems of *Mopalia muscosa* (SBMNH 83143) (a–f), *Nuttallochiton hyadesi* (SBMNH 83157) (g, h), and *Mopalia acuta* (i, j). Images d–f are of a ventral cast. All other images are of dorsal casts. a. Horizontal canals in pleural area and part of lateral area. b. Close-up of the jugal area showing flattened canals. c. Close-up of megalaesthete chambers and microaesthete canals. d. Slit ray canals. e. Apical area and ventral jugal triangle showing canals passing from the apical area into the ventral jugal triangle. Canals exiting at the lip of the apical area can also be seen. f. View of apical area showing microaesthete canals that originate at the apical area. g. Overview of valve cast showing little differentiation of valve areas. h. Close-up showing megalaesthete chambers. i. View of horizontal canals showing megalaesthete chambers and incompletely cast microaesthete canals (SBMNH 83160). j. Overview of half of valve cast (SBMNH 369432). Key: M = megalaesthete chamber; m = microaesthete canal; SRe = slit ray canals; all others abbreviations are shown in Figure 1.

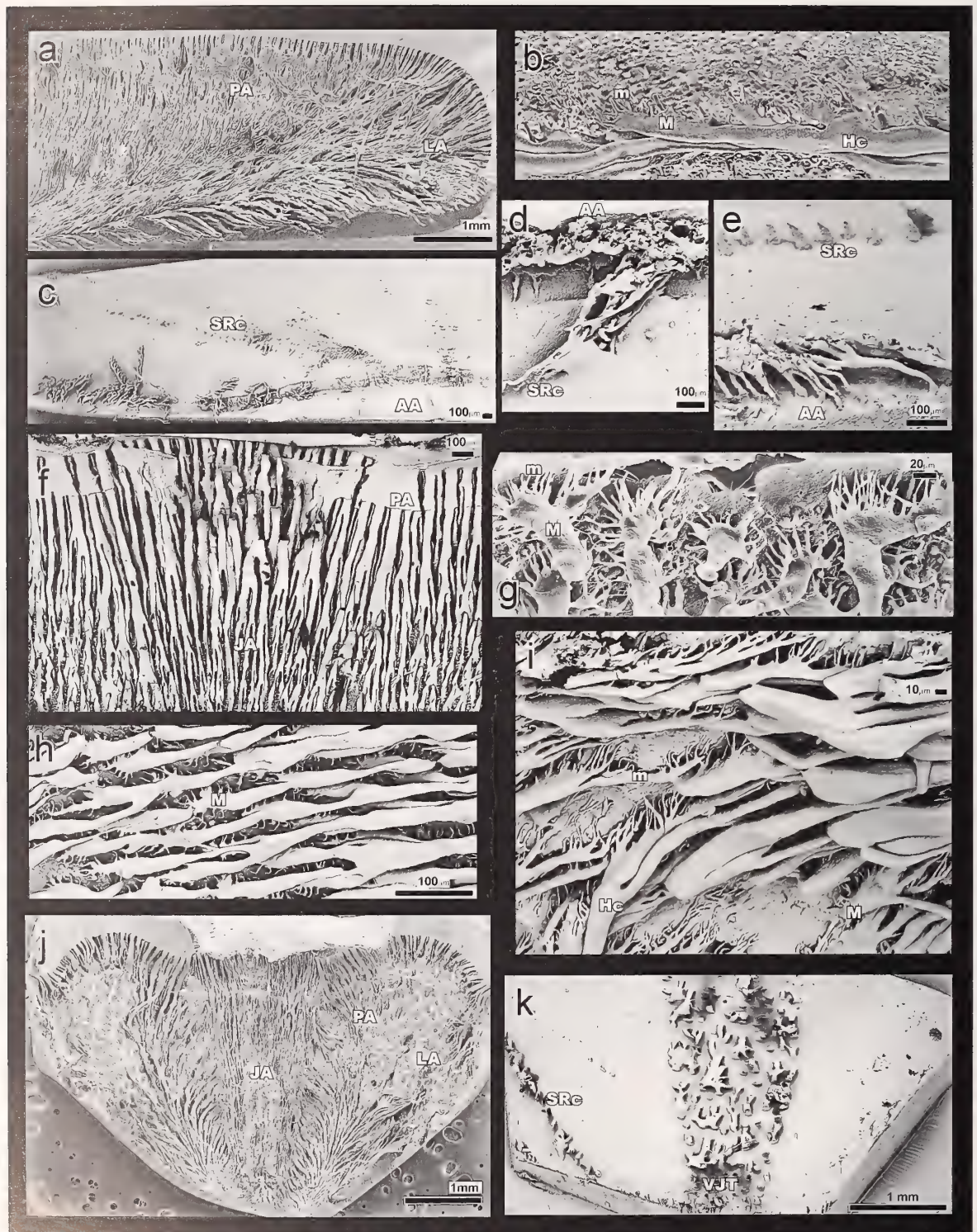


Figure 3. SEM images of casts of aesthete canal systems of *Placiphorella velata* (a–e), *Lepidochitona hartwegii* (f–h), and *Nuttallina californica* (i–k). Images c–e, k are of a ventral cast. All other images are of dorsal casts. a. Overview of half of cast showing little differentiation of valve areas (SBMNH 369440). b. Close-up of horizontal canals on same specimen, showing megal aesthete chambers and microaesthete canals. c. Overview of half of cast showing canals at slit ray region and apical area and partial canals at the ventral jugal triangle (SBMNH 83161). d. Magnification of canals at apical area passing into slit ray region.

in great detail. Numerous micraesthete-sized canals originate at the dorsal valve surface, merging with a larger subsidiary canal or with each other then with a subsidiary canal before then merging with a primary horizontal canal that exits at the anterior lip of the apical area. A few canals can be seen crossing from the apical area into the slit ray region.

Mopalia acuta (Acanthochitonina: Mopaliidae)

The dorsal casts (Figures 2i, j) reveal primary horizontal canals (~25–35 μm diameter) that run from the anterior to the posterior margin through all valve areas. There is a single principal layer of primary canals, with a density of ~19 canals per mm and a spacing of ~8–17 μm between the canals within this layer. Indistinct, elongate megal aesthete chambers (~8–17 μm diameter) feed into the main horizontal canals after a short length. The chambers merge along the length of the primary canals at regular intervals. Numerous micraesthetes (~1–3 μm in diameter) feed into each megal aesthete chamber all along its length.

On the ventral casts, growth lines as well as a few incomplete canals can be seen in the ventral jugal triangle. In one specimen, there is a line of partially preserved horizontal canals that parallel the slit ray, in addition to the apical area canals.

Nuttallochiton hyadesi (Acanthochitonina: Mopaliidae)

The dorsal casts (Figure 2g, h) reveal primary horizontal canals (~30–50 μm in diameter) that are preserved throughout the entire shell. There is a spacing of ~20–50 μm between canals, with ~18 canals per mm along the horizontal plane. Micraesthetes (1–3 μm diameter) feed into the elongate, indistinct megal aesthete chambers that feed directly, after a short distance, into the primary horizontal canals. This canal pattern is similar to that seen in the *Mopalia* spp. The megal aesthete chambers have a diameter of ~10–12 μm before widening to the same diameter as the connecting canals (~17–20 μm). At the region above the slit ray, the horizontal canals curve towards each other, merge, and proceed downward towards the slit rays.

The ventral casts reveal a narrow line of slit ray canals, apical area canals, but very few ventral jugal triangle canals.

Placiphorella velata (Acanthochitonina: Mopaliidae)

The dorsal casts (Figures 3a, b) reveal primary horizontal canals (~21–34 μm in diameter) that run from the posterior to the anterior margin through all valve areas. There is significant spacing between horizontal canals through much of the valve interior, but at the anterior margin, there are ~24 canals per mm with a spacing of ~22–40 μm between canals along the horizontal plane. At least two layers of primary canals can be seen. At regular intervals along the length of primary canals, there are junctions where short canals (~20–25 μm in diameter) from the megal aesthete chambers merge with the primary canal in a manner similar to that seen in *Mopalia acuta* and the other mopaliids. Numerous micraesthetes (~3–4 μm in diameter) feed into each elongate, indistinct megal aesthete chamber along its length. No obvious differences in aesthete canal morphology in the different valve areas can be detected in the casts.

On the ventral casts (Figures 3c–e), there are a few partial canals preserved at the ventral jugal triangle. There are also a number of slightly flattened canals scattered along the lines parallel to the slit rays. Canals are also preserved along the entire apical area. The canals turn upwards towards the dorsal valve surface and are oriented parallel to the direction of valve growth. They appear to originate as megal aesthete chambers close to the dorsal valve surface with two or more of these chambers merging into a single horizontal canal which exits at the apical area.

Lepidochitona hartwegii
(Acanthochitonina: Tonicellidae)

The dorsal casts (Figures 3f–h) reveal primary horizontal canals (~35–45 μm in diameter) that run from the posterior to the anterior margin through all valve areas. There is a spacing of ~15–35 μm between the primary canals, with ~20 canals per mm along the horizontal plane. The primary horizontal canals vary in diameter as they traverse the valve. At the posterior valve margin, many short lengths of subsidiary canals can be seen merging with each other to form a larger primary canal. As these primary canals continue to course towards the anterior margin, subsidiary canals merge into them at regular intervals. Megal aesthete

←

e. Close-up of apical area on same specimen showing canals turned up towards dorsal valve surface. A line of canals present at slit ray region can be seen behind the apical area. f. Overview of cast of *Lepidochitona hartwegii* (SBMNH 83146). g. Magnification of megal aesthete chambers and micraesthete canals (SBMNH 83147). h. Horizontal canals at posterior showing merging of megal aesthete chambers (SBMNH 83146). i. View of horizontal canals in same specimen, showing megal aesthete chambers and micraesthete canals. j. Overview of cast of *Nuttallina californica* (southern form; previously *N. fluxa*) (SBMNH 83149). k. Overview of cast of *Nuttallina californica* (SBMNH 83156) showing flattened canals at the ventral jugal triangle, slit ray region, and apical area. Key: Same as in Figures 1 & 2.

chambers that are typically elongate and indistinct, but occasionally with a slightly pear-shaped appearance, originate at the dorsal valve surface with a diameter of $\sim 10\text{--}14\text{ }\mu\text{m}$, then widen to a diameter of $\sim 25\text{--}30\text{ }\mu\text{m}$, before tapering off to $\sim 9.5\text{--}14\text{ }\mu\text{m}$ in diameter. Numerous micraesthete canals with a diameter of $6\text{--}9\text{ }\mu\text{m}$ merge into the megalaesthete chambers. Each micraesthete canal originates at a sub-spherical subsidiary cap. The megalaesthetes fuse into the horizontal canals after a short length.

There is some variation in canal morphology in the different valve areas. In the lateral and pleural areas, there is a shorter distance between megalaesthete chamber and primary canal than in the jugal area, where there is a longer distance and where many of the primary canals turn down towards the ventral valve surface.

The ventral casts show portions of flattened canals in the ventral jugal triangle and a few partial canals along the lines parallel to the slit rays, as well as apical area canals.

Nuttallina californica (Acanthochitonina: Tonicellidae)

The dorsal casts (Figures 3i, j) show an irregular spacing ($\sim 25\text{--}40\text{ }\mu\text{m}$ between canals) of primary horizontal canals ($\sim 20\text{--}40\text{ }\mu\text{m}$ diameter) packed at ~ 24 canals per mm along the horizontal plane. The primary canals run in a posterior-anterior direction at the jugal area and fan out diagonally at the pleural and lateral valve areas. There are some canals near the posterior margin of the valve that flank the jugal area, coursing inwards to form a v-shaped pattern. The most conspicuous primary canals are flattened with many tubular subsidiary canals ($\sim 12\text{--}15\text{ }\mu\text{m}$ in diameter) that feed into them. The subsidiary canals run above and subparallel to the primary canals. They begin at the dorsal valve surface as a megalaesthete chamber with a diameter of $\sim 6\text{--}10\text{ }\mu\text{m}$ and branch and widen to a range of diameters as they run into the primary canals. There are also numerous micraesthete canals $\sim 2.5\text{--}3.5\text{ }\mu\text{m}$ in diameter that merge all along the branching subsidiary canals. The megalaesthete chambers are not well defined, making it difficult to define where the megalaesthete chamber ends and the subsidiary canal begins.

At the jugal area, flattened horizontal canals appear to turn downwards towards the ventral valve surface. These canals appear to correlate with flattened, upward oriented canals found on the ventral jugal triangle of the ventral cast.

On the ventral casts (Figure 3k), a layer of large, flat canals can be seen overlying a lower layer of smaller, branching subsidiary canals in the apical area. Some of the large, flat canals extend from the apical area into the ventral jugal triangle. Numerous micraesthetes that originate at the apical area feed into subsidiary canals. There are also smaller and less flattened canals along

the lines parallel to the slit rays, some of which are turned upwards towards the dorsal valve surface, and others downwards towards the ventral valve surface.

There does not seem to be any significant difference in the aesthete canal systems between the southern form of this species (previously *N. fluxa*) and the northern form.

In addition to the aesthete canal system, the dorsal cast of one individual shows numerous borings produced by endolithic microorganisms. The clusters of borings are scattered among the aesthete canals located near the posterior end of the valve.

Lepidozonia mertensii (Chitonina: Ischnochitonidae)

The aesthete canal morphology seen in the dorsal casts (Figures 4a–d) correlates with the dorsal valve sculpture. Canals are arranged in discrete zones divided by linear regions that correlate with ridges on the valve surface. There is a v-shaped pattern of aesthete canals in the jugal area, a more parallel set of canals in the pleural area, and some canals that run diagonally from the slits to the apex of the valve in the lateral areas.

There is a single layer of primary horizontal canals close to the articulamentum layer. These primary canals vary in size ($\sim 15\text{--}30\text{ }\mu\text{m}$ in width) and shape, ranging from thin and round to thick and flattened. There are ~ 27 canals per mm along the horizontal axis, with a spacing of $\sim 20\text{--}40\text{ }\mu\text{m}$ between canals at the anterior margin. These primary horizontal canals connect the large, bulbous megalaesthete chambers. Each separated longitudinal zone of bulbous megalaesthete chambers in the lateral and pleural areas is approximately $5\text{--}7$ chambers wide. The ovoid megalaesthete chambers are oriented sub-parallel (angled slightly upwards) to the dorsal surface, with a maximum width of $\sim 35\text{--}45\text{ }\mu\text{m}$, tapering at each end to $\sim 7\text{--}10\text{ }\mu\text{m}$ in diameter. The chambers seem to either connect to a primary horizontal canal or to the body of a megalaesthete chamber adjacent to it. A number of micraesthete canals that start off at the valve surface at $5\text{--}7\text{ }\mu\text{m}$ in diameter and taper to $2\text{--}3\text{ }\mu\text{m}$ in diameter are located directly above the megalaesthete chamber and surround the megalaesthete canal that originates at the dorsal valve surface.

The ridges on the valve surface correspond with symmetrical pairs of megalaesthete chambers that have numerous micraesthetes feeding into them. The megalaesthete chambers in these areas are slightly larger than those in other regions of the valve.

The lateral areas lack the clearly defined longitudinal zones of megalaesthete chambers seen in the jugal and pleural areas. Instead, there are closely spaced megalaesthete chambers surrounding rows of pits that house large mound-shaped structures (assumed to be an extremely large megalaesthete chamber) with numerous micraesthete canals feeding into them. These pits correlate with the enlarged granules arranged in rows

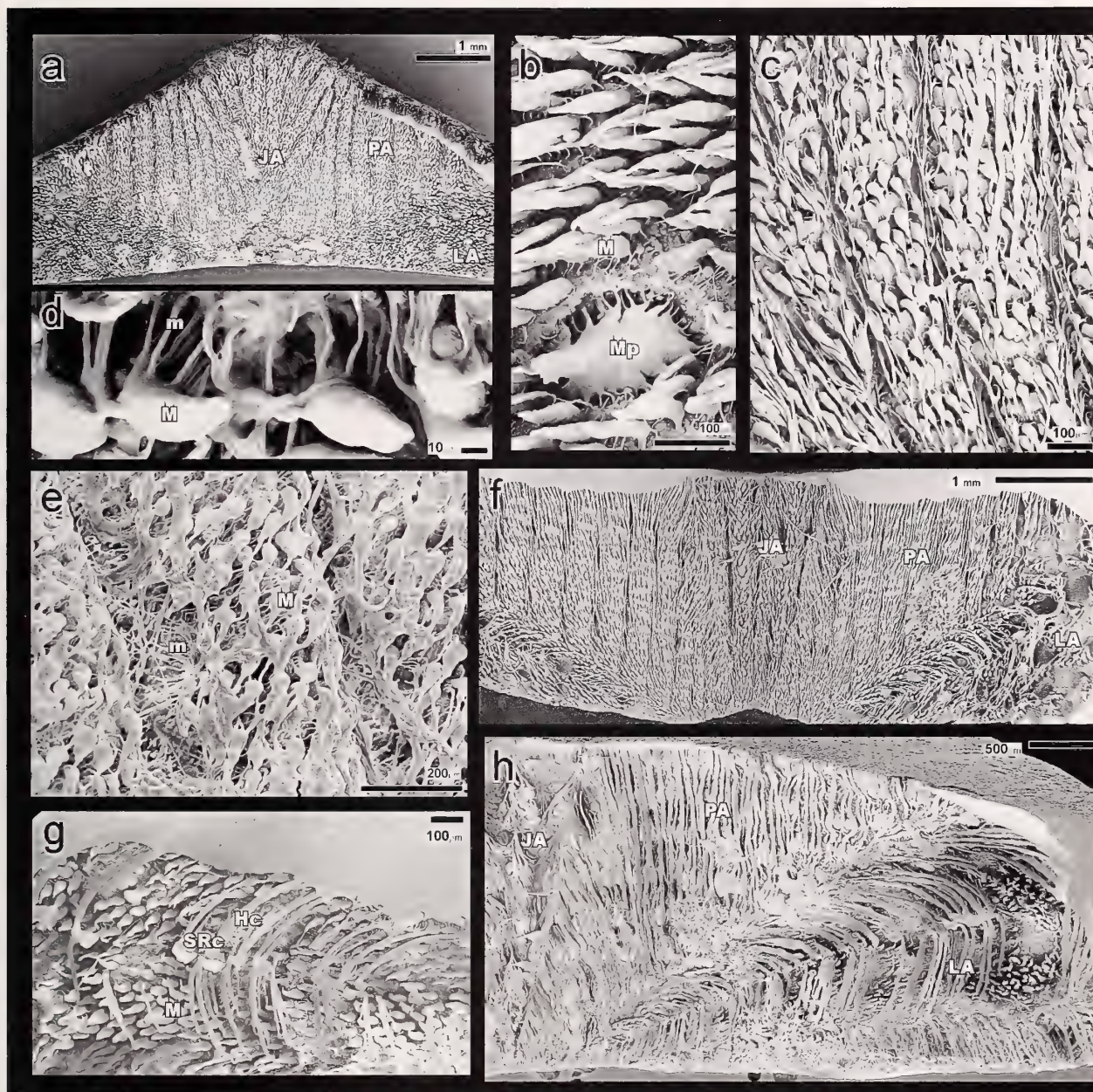


Figure 4. SEM images of casts of aesthete canal systems of *Lepidozonia mertensii* (a–d), *Lepidozonia cooperi* (e, f), and *Lepidozonia pectinulata* (g, h). All images are of dorsal casts. a. Overview of cast of *Lepidozonia mertensii* (SBMNH 83145) showing differentiated valve areas which correlate with valve sculpture. b. Megalaesthete chambers and megalaesthete pit located in lateral area in same specimen. c. Longitudinal columns of megalaesthetes with some flattened primary horizontal canals in same specimen. d. View of microaesthete canals and megalaesthete chambers in same specimen. e. View of *Lepidozonia cooperi* (SBMNH 83150) longitudinal columns of megalaesthetes with microaesthete canals. f. Overview of cast (SBMNH 83151) showing differentiated valve areas. g. View of *Lepidozonia pectinulata* (SBMNH 83152) showing lateral area with horizontal canals converging into slit ray canals. h. Overview of cast (SBMNH 83153) showing differentiated valve areas. Key: Mp = megalaesthete pit; all others same as in Figures 1 & 2.

on the dorsal valve surface. The megalaesthete chambers are oriented more perpendicular to the valve surface than their counterparts in the jugal and pleural areas.

On the ventral cast, canals are evident at the ventral jugal triangle, slit rays, and apical area. The small

portions of canals in the ventral jugal triangle are flattened and periodically turn up towards the dorsal valve surface. Canals at the slit rays seem to be thin and diagonally oriented towards the valve surface. Canals at the apical area are present along the entire width of

the posterior valve margin. Flat horizontal canals appear to exit at the anterior lip of the apical area and have many micraesthete canals which originate at the apical area feeding into them.

The slit ray canals consist of multiple rows that expand outward from the apex to the anterolateral margin. The jugal area canals are not abundant on the ventral casts.

Lepidozona cooperi (Chitonina: Ischnochitonidae)

The aesthete canal morphology of this species (Figures 4e, f) is similar to that of *Lepidozona mertensii*, except *L. cooperi* has a slightly greater proportion of horizontal canals. These canals are most noticeable along the anterior margin, and in the lateral areas. The thin, meandering horizontal canals curve towards each other in the lateral areas.

The ventral casts show a greater extent of jugal area canals preserved than in *L. mertensii*.

Lepidozona pectinulata (Chitonina: Ischnochitonidae)

The aesthete canal morphology of this species (Figures 4g, h) bears similarities to that of the other members of *Lepidozona* in this study. However, this species differs fundamentally from the other two species in that it lacks the huge esthete chambers in granule spaces and, more noticeably, has an extensive complement of large horizontal canals throughout much of the tegmentum interior. The curvature of these canals in the lateral area is more regular in *L. pectinulata* than in *L. cooperi*.

Ischnochiton textilis (Chitonina: Ischnochitonidae)

The dorsal casts (Figures 5a, b) reveal a canal system similar to that of *Lepidozona cooperi* and *Lepidozona pectinulata* in having horizontal canals that converge at the diagonal line and distinct, tear-drop shaped megal aesthete bulbs that feed into horizontal canals. There are ~29 primary horizontal canals (~9–23 μ m in diameter) per mm along the horizontal plane at the anterior margin. Primary horizontal canals are spaced ~15–27 μ m apart. These canals thin out towards the posterior margin, revealing rows of bulbous, sub-conical megal aesthetes above them. Micraesthete canals (~1–4 μ m in diameter) that originate at the dorsal surface merge into the ends of the megal aesthete chambers. The horizontal canals show a strong curvature in the pleural and lateral areas, and are straight in the jugal area.

The ventral casts reveal a high density of flattened canals present at the ventral jugal triangle and at the slit rays. Canals in the apical area are sparsely scattered along the posterior valve margin.

In one individual (SBMNH 83158), an unusual, probably secondary (see Discussion) pattern of large, bulbous cavities oriented sub-perpendicular to the shell

surface occur in the uppermost tegmentum layer. These cavities connect to tiny elongate canals that form a horizontal web just below the shell surface. Four way intersections of these tiny tunnels are present, although it is not clear if the intersections connect the large cavities to each other. The bulbous chambers (~40–50 μ m in diameter at origin, widening to ~53–60 μ m in diameter) have many small canals merging into them all along their height. The valves of this individual have occasional large openings on the dorsal surface that correspond to the bulbous cavities.

Ischnochiton variegatus (Chitonina: Ischnochitonidae)

On the dorsal casts (Figures 5c–e), there is evidence of two or more layers of primary horizontal canals. The top row of horizontal canals (~9–13 μ m in diameter), spaced approximately ~12–22 μ m apart from each other, can be clearly seen at the anterior valve margin. There are ~34 canals per mm along the horizontal plane at the margin. The dorsal casts reveal that micraesthete canals feed into teardrop-shaped megal aesthete chambers that taper down to connect to the primary horizontal canals. The primary canals are relatively thin, with low density, through much of the valve interior. The horizontal canals appear to be straight in the jugal area, curve slightly in the pleural areas (though to a lesser degree than in *I. textilis*), and have strong curvature in the lateral areas.

Both individuals examined showed the unusual, probably secondary (see Discussion) bulb and tunnel system in the uppermost portion of the tegmentum as described for the one individual of *I. textilis*. Above the primary horizontal canals, there is an interconnecting web of tiny, criss-crossing tunnels. Periodically, the small tunnels connect to the large, bulb-shaped cavities (~70–80 μ m in diameter at the origin, widening to ~80–120 μ m in diameter). There are approximately 15 bulbs per mm².

On the ventral cast, the ventral jugal triangle and lines parallel to the slit rays contain broken off canals. These partial canals are flattened and some are angled upwards towards the dorsal valve surface. There are also a few small diameter canals present in some regions of the apical area. Some canals in the apical area pass into the ventral jugal triangle and slit ray regions.

DISCUSSION

The casts reveal a remarkable degree of variation in morphology of the aesthete canals between species, families, and suborders of the Polyplacophora. This method of epoxy casting provides a unique way to observe the full morphology of the aesthete canal system in chitons. Moreover, the results of a cladistic analysis using only aesthete canal characters suggest that the aesthete canal system provides a suite of characters

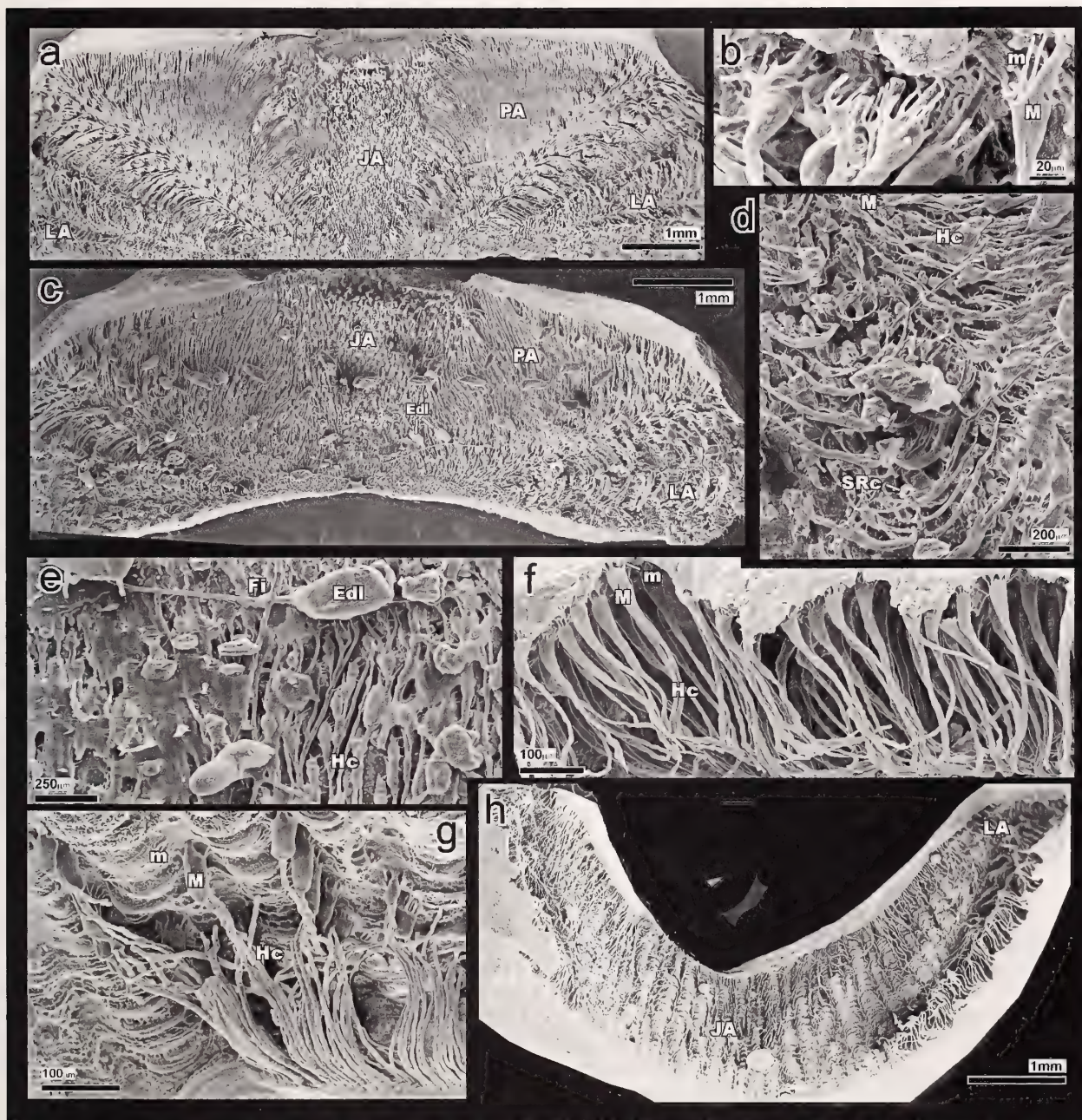


Figure 5. SEM images of casts of aesthete canal systems of *Ischnochiton textilis* (a, b), *Ischnochiton variegatus* (c–e), and *Lepidopleurus cajetanus* (f–h). All images are of dorsal casts. a. Overview of cast of *Ischnochiton textilis* (SBMNH 369435) showing some differentiation of pleural and lateral areas. b. Close-up of megalaesthete chambers surrounded by microaesthetes in same specimen. c. Overview of cast of *Ischnochiton variegatus* (SBMNH 369437) showing some differentiation of pleural and lateral areas. d. View of lateral area showing slit ray canals in same specimen. e. Close-up view of pleural area in same specimen showing endolithic borings. A four-way endolith tunnel intersection can be seen. f. View of *Lepidopleurus cajetanus* (SBMNH 83154) showing megalaesthete chambers at posterior margin. g. Magnified view of microaesthete canals and megalaesthete chambers in same specimen; note the single rows of megalaesthete chambers. h. Overview of cast of same specimen. Key: Edl = Endolith boring; Fi = four way intersection; all others same as in Figures 1 & 2.

useful in future taxonomic and phylogenetic analyses of chitons, confirming preliminary conclusions to this effect by Fernandez et al. (1999), which were also reported in Vendrasco et al. (2006).

The proportion of the entire aesthete canal system replicated in the casts appears to have varied slightly from species to species and to a lesser extent from individual to individual. In a few cases, large portions of canals in certain regions are missing. However, we examined at least two valves of at least two individuals of each species except for *Nuttallochiton*, and observed consistent canal infiltration patterns. Therefore, it seems most likely that the apparent incomplete cases of canal replication are due in part to an original low density or a natural closure of portions of the canal system during the life of the chiton. Also, some canal casts may have broken off during processing of the specimens (e.g., splitting dorsal from ventral cast). Regardless, the valve casts are complete enough to allow an accurate reconstruction of the entire aesthete canal system.

The casts reinforce many of the observations that Leloup made about the aesthete canals at the shell surface of numerous chiton species. For example, Leloup (1934) described that the aesthetes in *Lepidopleurus cajetanus* are clustered on the valve surface, with each megalaesthete associated with ~7–10 micraesthetes, and with the megalaesthete more centrally located in each cluster in the lateral areas compared to the central area. These results are consistent with what we found. In addition, for *Mopalia muscosa*, the flared-end, trumpet tube shape of the megalaesthetes, the size proportions of micraesthetes and megalaesthetes, and elongate nature of near-surface canals that the micraesthetes and megalaesthetes feed into, as revealed by these casts, are similar to what Leloup (1940) drew for this species. In *Mopalia acuta*, the relative sizes and shapes of the micraesthetes and megalaesthetes revealed by these casts are also similar to what Leloup (1942) illustrated for this species. In *Lepidochitona hartwegii*, the relative width of the megalaesthete chambers, the large number of micraesthetes per megalaesthete, and the lack of much separation between micraesthetes from adjacent chambers as revealed by these casts and valve surface observations are all similar to what Leloup (1940) illustrated for this species. In *Nuttallina californica*, the disparity in sizes between megalaesthetes and micraesthetes, the large number of micraesthetes, and the relative spacing between aesthetes, as revealed by the casts and surface observations, are similar to what Leloup (1940) described for this species, although in his drawings the micraesthetes are a bit less regularly spaced, and he drew bulbous megalaesthete chambers, not the unusual elongated near-surface canals that our casts reveal. In *Lepidozona mertensii*, the shape and orientation of the

megalaesthetes and associated micraesthetes as revealed by these casts are similar to what Leloup (1940) illustrated for this species. In addition, the huge megalaesthete chambers associated with granules in *L. mertensii* were also illustrated by Leloup (1940). However, in *Placiphorella velata*, the megalapores are only slightly larger than the micropores, as seen in an examination of the shell surface and in the dorsal casts of the canal system. This contrasts with the drawing of the pore system of *P. velata* in Leloup (1942), which shows distinctly larger megalapores.

Phylogenetic Utility of Aesthete Canal Characters

Figure 6 shows how the results of a cladistic analysis based only on aesthete characters matches a recent hypothesis of chiton phylogeny, with members of the same family (based on the taxonomy presented in Sirenko, 1993 and 1997) grouping together in the resultant cladogram. Sirenko's taxonomy was used because it is largely supported by phylogenetic analyses using morphology (Buckland-Nicks, 1995) and molecular data (Okusu et al., 2003). Figure 6 reveals that there are clear differences between the aesthete canal systems of chitons of the sub-order Chitonina and those of the Acanthochitonina. Moreover, members of each family share derived aesthete canal characters in common.

In addition to the results of this cladistic analysis, the canal system of *Lepidochitona cinerea*, as drawn by Knorre (1925), is similar in many respects to that of *Lepidochitona hartwegii* as revealed in this study. Both show the uniquely-shaped, elongate megalaesthete chambers that have numerous micraesthetes feeding into them along their length, and that feed directly, after a short length, into the main horizontal canals at regular intervals. Moreover, Knorre (1925) drew a small portion of the aesthete canal system in *Ischnochiton herdmani*, which Kaas & Van Belle (1994) later synonymized with *Stenoplax alata*, and the presence of megalaesthete bulbs evenly spaced that feed via long stalks into thin, widely-spaced horizontal canals is quite similar to that of the ischnochitonids in this study. In addition, the aesthete canal system revealed for *Chiton albolineatus* by Haas & Kriesten (1978) differs substantially from that of any of the taxa in this study, none of which is thought to be in the same family as *Chiton*.

There is a difference of opinion, however, on assignments to families between Sirenko (1997) and Kaas & Van Belle (1994), and those suggested from the results of (Okusu et al., 2003). In particular, the assignment of *Nuttallochiton* to the Mopaliidae is not supported by (Okusu et al., 2003) or Kaas & Van Belle (1994). Also, Thiele (1931) argued that *Nuttallochiton* belongs in the family Lepidochitonidae, but he also

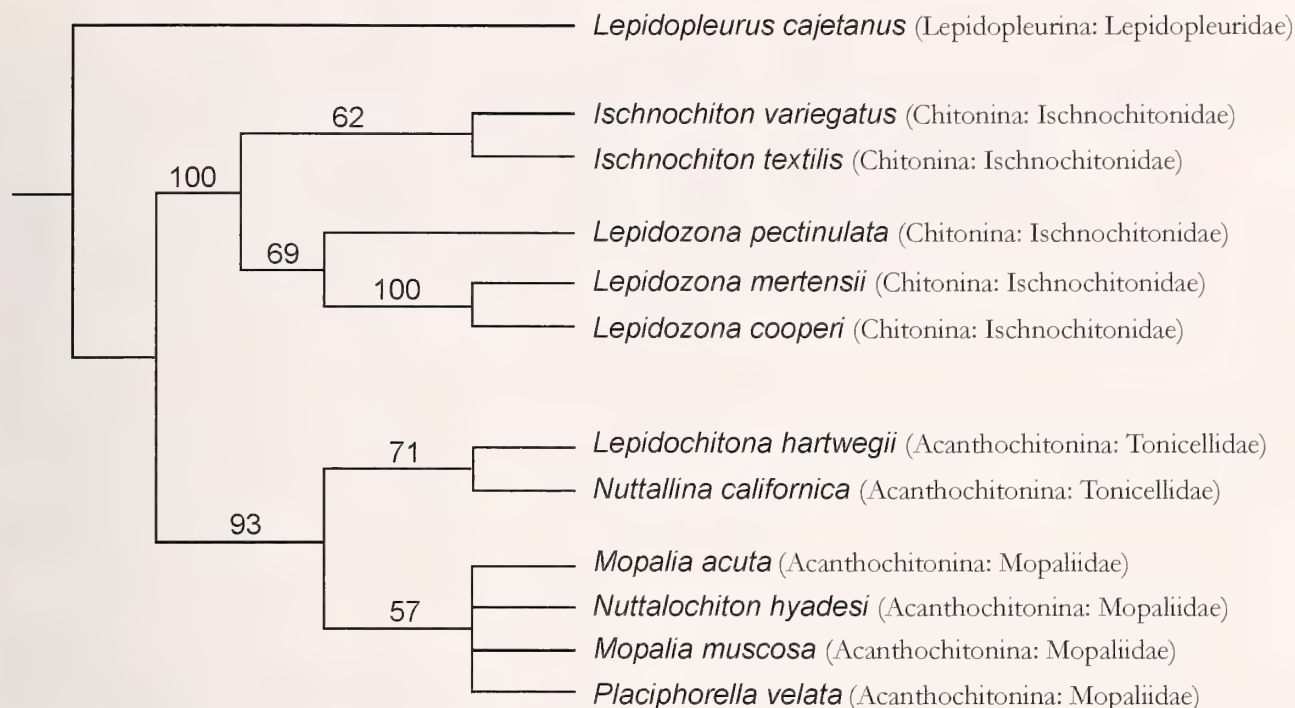


Figure 6. Majority rule consensus of the 42 most parsimonious trees. Numbers indicate the frequency of occurrence of the branch in the 42 trees. Assignments to chiton suborders and families (in parentheses) are based on Sirenko (1997). The data matrix for the analysis is shown in Table 1 and the characters and character states are listed in Table 2.

argued that *Lepidopleurus* belongs in this family so his concept of the Lepidochitonidae was quite broad. Our results are in line with Sirenko's (1997) hypothesis.

Nuttallina and *Lepidochitona* were placed in the family Tonicellidae by Sirenko (1997). Oldroyd (1927), Thiele (1931); E. P. Chace (1940), and Ferreira (1982) had previously placed both genera in the family Lepidochitonidae. However, the results of Okusu et al. (2003) suggest a close relationship between *Lepidochitona* with members of the Mopaliidae, although they did not include *Nuttallina* in their analysis. A. Myra Keen (1963) placed *Lepidochitona* in the Ischnochitonidae, united with *Lepidozonia*, *Ischnochiton*, and others, and she placed *Nuttallina* in the separate Family Callistoplacidae. Kaas & Van Belle (1994) also placed *Nuttallina* and *Lepidochitona* in the Ischnochitonidae. The data from the aesthete canal system in this paper support the linkage of these two genera, and are consistent with a close relationship with the mopaliids, but do not support the inclusion of *Lepidochitona* and *Nuttallina* in the family Ischnochitonidae.

The aesthete canal system of *Lepidopleurus cajetanus* is unique in a few ways compared to the other chitons in this study: it has rows of megal aesthetes, one or two wide, in the central area, and each megal aesthete feeds directly into a thin, meandering canal that interweaves

with others on the way towards the anterior or lateral margin.

The ischnochitonids, even though found on separate continents and with different valve sculptures (*Ischnochiton textilis*, Africa; *Ischnochiton variegatus*, Australia; *Lepidozonia* sp., North America), have similar canal systems that are largely different from those seen in the other species in this study. They each possess subconical megal aesthete chambers and a distinctly different aesthete canal form in the lateral area compared to central area. We interpret the huge bulbs distributed throughout the tegmentum of both individuals of *I. variegatus* and one individual of *I. textilis* are interpreted not as ocelli-bearing cavities, but as having been produced by an endolithic microorganism, because of their unusual shape, the lack of any connection to a primary horizontal canal, their connection to a web of tiny, intersecting horizontal tunnels that do not look like aesthete canals, and their absence in one individual of *I. textilis*.

The mopaliids, by contrast, all have large, closely spaced primary horizontal canals that exist within much of the valve interior as well as regular merging of subsidiary branches with the primary canals. Both tonicellids have a greater frequency of merging of subsidiary canals in the posterior portion of the valve

Table 1

Discrete aesthete characters used in the PAUP analysis. Descriptions of characters and character states provided in Table 2.

Species	1 agc	2 are	3 blb	4 mcr	5 mhc	6 deh	7 hmc	8 hcc	9 apz	10 mgc	11 doc
<i>Lepidopleurus cajetanus</i>	1	0	1	0	0	0	0	0	1	2	0
<i>Mopalia muscosa</i>	0	0	0	1	1	2	0	0	0	0	2
<i>Mopalia acuta</i>	0	0	0	1	1	2	0	0	0	0	2
<i>Placiphorella velata</i>	0	0	0	1	1	1	0	0	0	0	2
<i>Nuttalochiton hyadesi</i>	0	0	0	1	1	2	0	0	0	0	1
<i>Lepidochitona hartwegii</i>	1	0	0	2	0	2	0	0	0	0	?
<i>Nuttalina californica</i>	1	0	0	2	0	2	0	0	0	0	2
<i>Lepidozона mertensii</i>	0	1	1	0	0	1	1	?	1	1	?
<i>Lepidozона pectinulata</i>	0	1	1	0	0	1	0	1	1	1	1
<i>Lepidozона cooperi</i>	0	1	1	0	0	1	1	1	1	1	1
<i>Ischnochiton variegatus</i>	0	1	1	0	0	1	0	1	0	1	1
<i>Ischnochiton textilis</i>	0	1	1	0	0	1	0	1	0	1	1

to form the primary horizontal canals, and a correlation between the megalapores and granules.

The results suggest that many aesthete canal characters may be useful for future phylogenetic studies. However, some other aesthete characters seem to be less phylogenetically significant. For example, Currie (1989) argued that average pore density on the upper valve surface, as well as the micropore/megalapore ratio, did not show tight correlation with phylogeny in the four Australian species that he examined. Future comparisons of aesthete canal character state distributions in a wider range of taxa will better determine the phylogenetic utility of such characters.

Environmental Influence on Aesthete Canal Patterns

Currie (1992) argued that the diversity of aesthete complexity suggests the capacity to perform a variety of functions. However, he found that the fine structural detail of different aesthete classes showed no significant differences between chiton taxa, leading him to argue that aesthete canal differentiation is of little importance in affording a range of functions.

Some of the aspects of the biology of the chiton species in this study are shown in Table 3. There seems to be little correlation between aspects of ecology and

Table 2

Aesthete characters and character states for the PAUP analysis.

#	Code	Description of character	0	1	2
1	agc	aesthete/granule correlation	none apparent	one megalapore per granule	
2	are	megalaesthete canal morphology/pattern differ by valve area	absent	present	
3	blb	megalaesthete bulbs in central area	indistinct	distinct	
4	mcr	micraesthetes feeding into subsidiary canals along their length	absent	present	only near "megalaesthete"
5	mhc	connection between surface and main horizontal canals	long canal	short canal	
6	deh	density of horizontal canals in middle to posterior	very low (much visible space between canals)	low (some visible space between canals)	high (little visible space)
7	hmc	huge aesthete chambers in large granules	absent	present	
8	hcc	degree of horizontal canal curvature towards diagonal line	none to low	medium	high
9	apz	canals differentiated into anterior-posterior columns	indistinct	distinct	
10	mgc	typical megalaesthete chamber shape	non-differentiated from canal	bulbous teardrop	bulbous sausage
11	doc	direction of convergence of horizontal canals in lateral area	no clear convergence	converge towards anterior	converge towards posterior

Table 3
Information on ecology for the twelve species used in this analysis.

Species	Depth	Habitat	Other comments	References
<i>Mopalia muscosa</i>	Intertidal zone.	Wet, protected large crevices; high protected tidepools; usually in direct contact with moisture. Also exposed on surfaces of rocks in high energy environments.	Valves often covered; active at night; negatively phototactic when young.	Andrus & Legard, 1975; Kaas & Van Belle, 1994; Fitzgerald, Jr., 1975; Smith, 1975; Liff-Grieff, 2006; personal observation.
<i>Mopalia acuta</i>	Intertidal to 40 m.	Under rocks on cobble reef; in cracks and crevices protected from the sun.	—	Collection data, 1970; Kaas & Van Belle, 1994; Liff-Grieff, 2006.
<i>Placiphorella velata</i>	Shallow subtidal to 20 m; occasionally intertidal.	Flat sides of movable rocks or upside down under boulders; in crevices or walls of deep tidepools; in sea urchin excavations in bedrock.	Carnivorous; avoids light; always in shade; shell plates often covered with organisms.	Andrus & Legard, 1975; Mclean, 1961; Clark, 1991, 1994; Kaas & Van Belle, 1994.
<i>Nuttallochiton hyadesi</i>	20 m +	In deep water (up to at least 400 m).	—	Kaas & Van Belle, 1994.
<i>Lepidochitona hartwegii</i>	Upper intertidal (usually) to 17 m.	Under <i>Silvetia compressa</i> fronds or less commonly under <i>Fucus distichus</i> ; also occur in small, wet crevices or depressions in the upper intertidal, or in tidepools in the upper intertidal.	Negatively phototactic; most active at night while dry or in wash. Valves often eroded.	Lyman, 1975; Andrus & Legard, 1975; Eernisse, 1984, 1986; Kaas & Van Belle, 1994; Liff-Grieff, 2006; personal observation.
<i>Nuttallina californica</i>	Upper and middle intertidal zone.	In exposed habitat on top of rocks—wedged in small crevices or grooves in high shallow tidepools; squeezed between bases of <i>Tetracilia squamosa reubescens</i> , <i>Pollicipes polymerus</i> , and <i>Mytilus californicus</i> .	At rest during low tide; grazing during high tide; lives in oval pits created by radular scraping. Valves often eroded.	Andrus & Legard, 1975; Piper, 1984; Kaas & Van Belle, 1994; Liff-Grieff, 2006; personal observation.
<i>Lepidozona mertensii</i>	Intertidal to 100 m.	Under rocks.	Negatively phototactic.	Ferreira, 1978; Ricketts et al., 1985; Kaas & Van Belle, 1994; personal observation.
<i>Lepidozona cooperi</i>	Intertidal to 20 m.	Under rocks.	Negatively phototactic.	Ferreira, 1978; personal observation.
<i>Lepidozona pectinulata</i>	Intertidal to 20 m.	Under rocks.	Negatively phototactic.	Ferreira, 1978; personal observation.
<i>Ischnochiton variegatus</i>	Intertidal to shallow subtidal zone.	Under small rocks with sand.	—	Collection data, 1972; Kaas & Van Belle, 1994.
<i>Ischnochiton textilis</i>	Intertidal to shallow subtidal zone.	Under rocks.	—	Kaas & Van Belle, 1994; Sliker, 2000.
<i>Lepidopleurus cajetanus</i>	Typically in intertidal zone; ranges to 40 m.	On stones, rocks, and old shells	Unslit insertion plates.	Smith, 1960; Kaas & Van Belle, 1994.

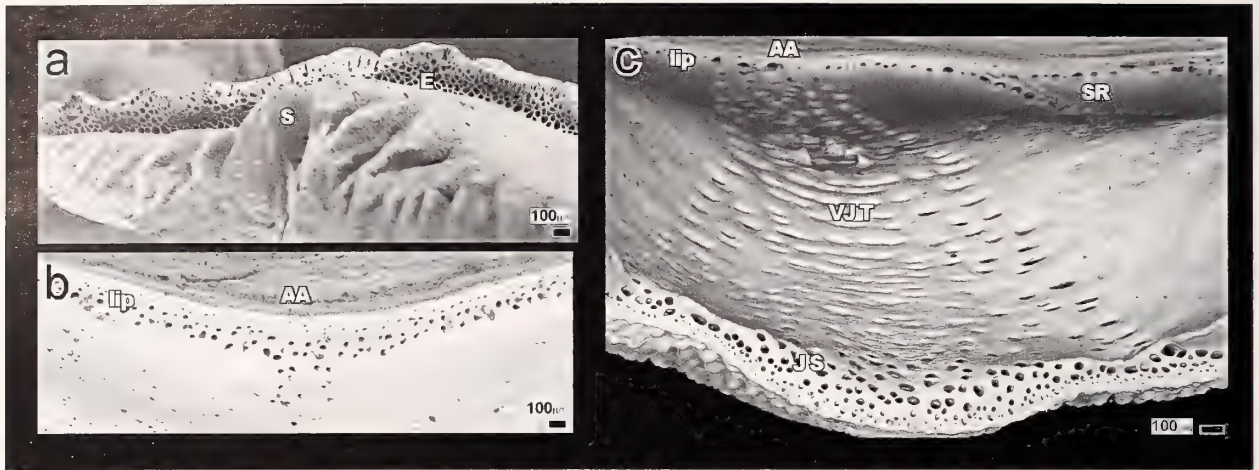


Figure 7. SEM images of valves. a. Eaves of *Mopalia muscosa*. b. Ventral valve surface showing apical area of *Mopalia muscosa* showing pores at lip. c. Ventral valve surface of *Nuttallina californica* showing pores at jugal sinus, ventral jugal area, and lip of apical area. Key: E = eaves; all others same as in Figure 1.

those of the aesthete canal morphology revealed in this study. Many of the species in this study share similar habitats and depth preferences (e.g., many are intertidal or have a wide depth range) but have different aesthete canal patterns. Likewise, the mopaliids in this study occupy different environments (*Mopalia muscosa* and *Mopalia acuta* in the intertidal; *Placiphorella* in the shallow subtidal; and *Nuttallochiton* in deep water) and yet show striking similarities in aesthete canal morphology.

Other Influences on Aesthete Canal Patterns

Some aspects of the form of the aesthete canal system are likely to be influenced by the shell layers in which they occur. The slit ray and ventral jugal triangle canals have a flattened appearance in all casts where they were preserved. Perhaps this is due to the fact that these canals pass through the denser articulamentum. Interestingly, at the jugal sinus, pores with a circular cross-section can clearly be seen (Figure 7c); these connect to the flattened canals in the valve interior.

Also noticeable is a correlation between the thickness of the tegmentum and the number of levels of the canal system. This is evidenced by the multiple rows visible at valve eaves (Figure 7a), as well as the multiple levels seen most clearly along the anterior margin of the casts. For example, the *Ischnochiton* species in this study have a thin tegmentum and so have only two levels of horizontal canals while the *Nuttallina californica* and *Mopalia muscosa*, which both have a thicker tegmentum, have more than two layers of horizontal canals.

Currie (1992) argued that aesthete canal differentiation in the three Australian species he examined may

represent inherent differences in shell growth associated with the formation of major valve sculptures. Similarly, *Lepidozona mertensii*, *Lepidozona cooperi*, and *Lepidopleurus cajetanus* show a strong connection between the aesthete canal system and valve sculpture (Figure 4a), with spaces in the canal system corresponding to ridges and granules on the dorsal valve surface. However, *Ischnochiton variegatus* has a similar valve shape and sculpture to that of *L. mertensii*, but lacks the corresponding spaces within its aesthete canal system. Along these same lines, there is a diversity of valve sculptures within the mopaliid and *Ischnochiton* species in this study, but the mopaliids each have a strongly similar aesthete canal morphology to each other, as do the *Ischnochiton* spp.

Connectivity of the Aesthete Canal System in the Apical Area

Many slit ray and ventral jugal triangle canals seem to connect to those in the apical area (seen in the casts of *Mopalia muscosa* and *Placiphorella velata*) and there is evidence in these regions for a direct connection between upper and lower valve surfaces (seen in the casts of *Mopalia muscosa* and *Nuttallina californica*), as postulated by Baxter & Jones (1981). Canals in the apical area seem to be more complicated than was previously appreciated. For example, canals seem to originate at the apical area itself rather than just from the dorsal valve surface above the apical area. Additionally, in some species, canals exit at the lip of the apical area, evidenced by the canals in the cast (seen in *Nuttallina californica* and *Mopalia muscosa*) and the presence of pores in this area of the valves (Figure 7b).

Conclusions

This method of embedding chiton valves has proven remarkably effective at revealing the three-dimensional morphology of the aesthete canal system. Inferences from these casts allow detailed comparisons between the twelve taxa in this study. The casts reveal that: (1) both large and small-scale canal morphologies are highly variable between the nine species examined; (2) the variation shows a much stronger correlation with phylogenetic relationships than with ecological factors; (3) there is a high degree of connectivity in the total aesthete canal system; and (4) canal morphology seems also to be strongly influenced by the shell layer and region in which the canals occur, confirming results by previous authors.

The results suggest that the aesthete canal system provides a suite of characters that are useful in phylogenetic and taxonomic studies of chitons at the species level (note in particular the differences between members of *Lepidozona*) and even more useful at higher taxonomic levels. Future embedding of valves of species within other chiton families will allow a better assessment of the extent of this utility throughout the Polyplacophora.

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Morphologic and Reproductive Biology of Two Species of the Buccinid Gastropod Genus *Aeneator* Finlay, 1927 from Southern Chilean Fjords

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Abstract. The present study describes new records for the buccinid gastropods *Aeneator fontainei* (D'Orbigny, 1841) and *Aeneator loisae* Redher, 1971 collected in Chile's southern fjord region in 2001 and 2002. This report now extends the distribution of these species to 46°S. Observations on the morphologies of their egg capsules showed intraspecific differences in form, presence of indentations on the borders and location of the pore. Differences were also noted between the juveniles' shell apertures of the two species; in *A. fontainei* the border is smooth and sharpened, while in *A. loisae* it is undulant due to the presence of exterior ribs. One intracapsular specimen of *A. fontainei* shows the presence of a penetration on the last shell whorl. This perforation exhibited marked denticulations when viewed in the scanning electron microscope, suggesting the occurrence of intracapsular cannibalism by the juvenile snails. It was concluded that these species have direct holobenthic development.

INTRODUCTION

The present study presents new data on neogastropod molluscs of the family Buccinidae. This family has representatives in most of the world's oceans, from the poles to the equator, and inhabits a wide variety of mainly marine environments (Hayashi, 2005). It is one of the most diverse and abundant families of caenogastropods represented by 120 genera with at least 1000 species in the world (Vaught, 1989; Kantor, 2003). There are 14 genera present on the Pacific coast of north and South America from Baja California to Perú and northern Chile (Keen, 1971). McLean and Andrade (1982), revised the taxonomy of the genus *Aeneator* whose species are known from New Zealand and Chile. The buccinids of the present study include *Aeneator fontainei* (D'Orbigny, 1841), the most common Chilean species of the group, and *Aeneator loisae* Redher, 1971. This last species was included in subgenus *Ellicea* Finlay, 1927, which was reduced to synonymy by Powell (1979) (*vide* McLean & Andrade, 1982).

A. fontainei has been reported from Bahía Independencia, Perú (14°13'S) to Punta Toro, Chile (33°01'S) and *A. loisae* from Coquimbo (29°58'S) to Cabo Carranza (35°27'S), Chile (McLean & Andrade, 1982).

At present, reproductive aspects such as the pattern of oviposition, morphology of capsules (Gulbin, 2000; Martell et al., 2002), larval protoconch and soft parts such as stomach characters (Kantor, 2003) and penis morphology (Harasewych & Kantor, 2002) are specific characteristics of important taxonomic value, especially among the neo and mesogastropods. Knowledge of the reproductive aspects of Chilean gastropods is limited to

a few subtidal species from the northern Chilean coast. One of the best studied of the muricids is *Chorus giganteus* Lesson, 1830, which inhabits subtidal soft-bottom muddy sands and deposits its egg capsules on shells of congeners, in which larval stages develop through to eclosion and release of benthic-feeding juvenile snails (Gallardo, 1980).

Biological data on *A. fontainei* and *A. loisae* are scarce and primarily restricted to morphological characteristics of their shells (D'Orbigny, 1841; McLean & Andrade, 1982; Ramirez, 1990; Guzman et al., 1998); some population data also exists (Alarcon et al., 1999). The objective of the present study is reporting the occurrence of these two species in Chile's fjord region, thus extending their known geographic range by 10° in latitude. An attempt has also been made to add to the knowledge of their adult morphology and to present new data on their egg capsules and the morphology of intracapsular juveniles.

MATERIALS AND METHODS

Data and biological material were collected during Cimar Bio-oceanographic cruises 7 and 8 (Osorio et al., 2005; Osorio et al., 2006) which formed part of the "Biodiversity of Austral Fjords" projects sponsored by the Chilean Naval Oceanographic Committee (Comité Oceanográfico Nacional de Chile). The cruises visited inshore waters between 43°45'S and 46°05'S on July 2001 and 2002. Samples containing molluscs were fixed in 10% formalin-seawater, and later stored in 70% alcohol for subsequent identification. Adult specimens of *A. fontainei* and *A. loisae* were photographed and

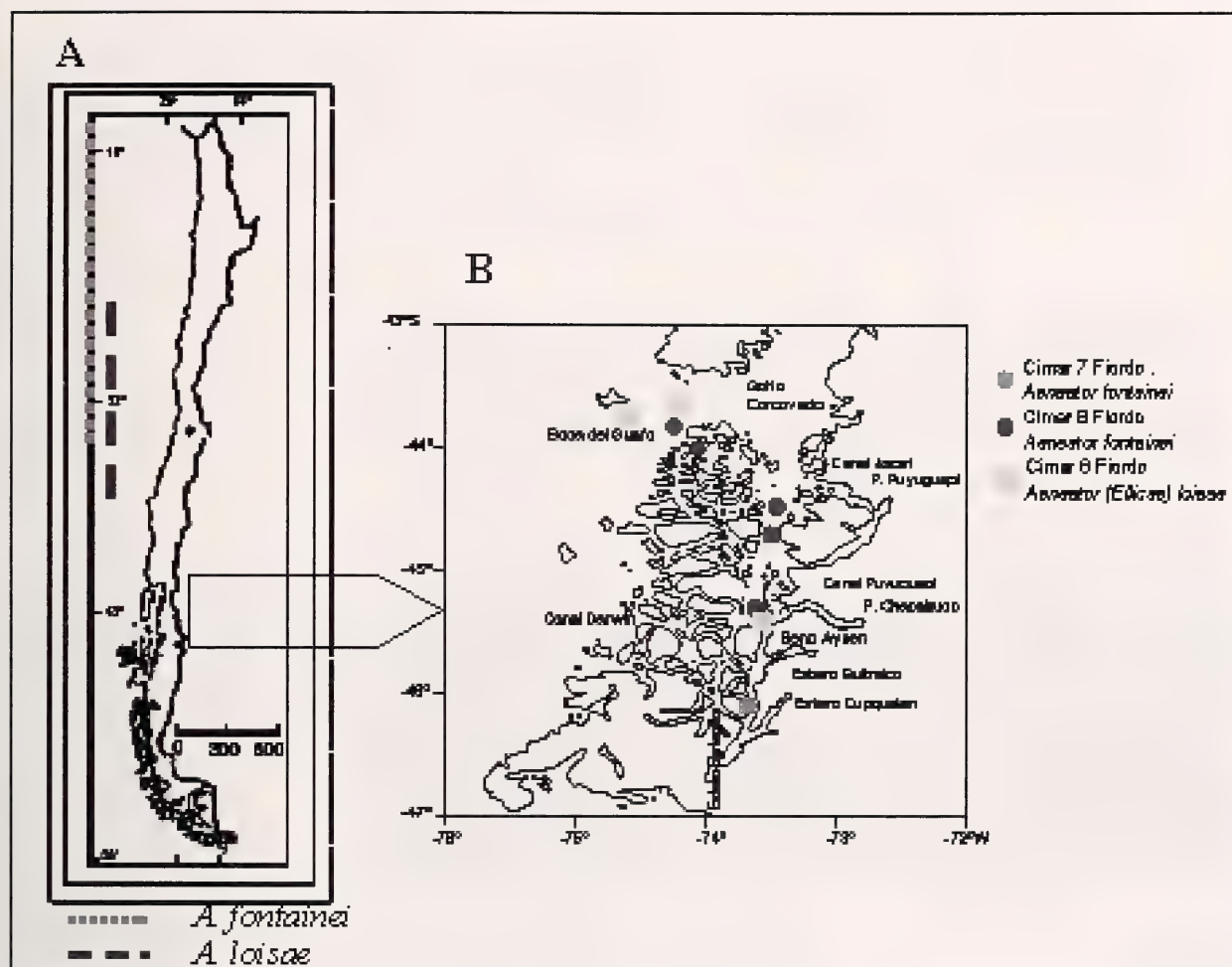


Figure 1. A. Original geographic distribution of *A. fontainei* and *A. loisae* and location of the Chilean austral fjord region. B. Amplification of the distribution of *A. fontainei* and *A. loisae* as a result of collections made during CIMAR fjord cruises 7 & 8.

measured with vernier calipers. Shell length is the maximum dimension parallel to the axis of coiling, shell width the maximum dimension perpendicular to length. The morphology of the egg capsules of these snails was described using drawings made with a camera lucida attached to a Leitz stereo microscope. A total of 32 capsules from *A. fontainei* and one capsule from *A. loisae* were opened centrally to obtain the contained larvae for morphological observation. Later, the egg capsules and juveniles of both species were measured with a camera lucida and scale, to 0.01 mm, using an ocular micrometer in the stereo microscope and also photographed using a dark field in conjunction with both reflected and transmitted light. The juveniles were also observed and photographed using a Zeiss DS M 940 scanning electron microscope (SEM). The location of voucher specimens is Museo Nacional de Historia Natural (Chile), collection numbers: 5687 to 5696.

RESULTS

Six individuals of *A. fontainei* were obtained, of which two were adults, and four *A. loisae* of which three were adults. These findings represented a new record for the presence of these species in this region, with *A. fontainei* at more than 13° and *A. loisae* at more than 10° farther south than previously recorded (Figures 1A, B). Geographic locations and oceanographic data for each individual of the two species collected are listed in Table 1.

Shell Measurements

The sizes of the shells of the adult specimens of *A. fontainei* ranged from 10.3 to 12.8 cm, while those of *A. loisae* were from 10.5 to 12.8 cm in total length (Figures 2A, B). Table 2 presents the details of the

Table 1

Number of specimens observed with corresponding oceanographic data for *A. fontainei* and *A. loisae* obtained during CIMAR Fjord cruises 7 and 8.

Species	Number of specimens	Locality	Date	Latitude (south)	Depth (m)	Temperature (°C)	Salinity (‰)
Cruise CIMAR Fjord 7							
<i>A. fontainei</i>	1	Estero Elefantes	07/2001	46°05,01'	60	9.3	28.09
Cruise CIMAR Fjord 8							
<i>A. fontainei</i>	1	Canal Moraleda	07/07/2002	44°25,30'	200	*	*
	1	Canal Moraleda	07/07/2002	44°40,80'	345	10.1	33.52
	1	Canal Moraleda	07/07/2002	45°21,20'	75	9.7	31.25
	1	Canal Tuamapu	20/07/2002	44°00,00'	220	9.9	33.31
	1	Canal Tuamapu	20/07/2002	43°58,50'	160	9.9	33.45
<i>A. loisae</i>	1	Boca del Guafo	06/07/2002	43°45,20'	230	9.6	34.04
	2	Boca del Guafo	06/07/2002	43°41,00'	200	9.8	33.94
	1	Canal Moraleda	07/07/2002	45°21,20'	75	10.1	33.51

* No information



Figure 2. **A.** *A. fontainei* with three rows of egg capsules deposited on its shell. **B.** *A. loisae* with egg capsules deposited on its shell.

Table 2
Size, sex, and observations on *A. fontainei* and *A. loisae* from Table 1.

Species	Length (cm)	Width (cm)	Sex	Observations
Cruise CIMAR Fjord 7				
<i>A. fontainei</i>	10.3	4.5	F	Alive with egg capsules
Cruise CIMAR Fjord 8				
<i>A. fontainei</i>	2.4	1.0	—	No presence of soft parts
	3.9	2.0	—	No presence of soft parts
	12.8	5.5	M	Alive
<i>A. loisae</i>	10.5	5.0	M	Alive with egg capsules
	12.8	6.3	M	Alive with egg capsules
	11.9	5.7	—	No presence of soft parts
	2.2	1.0	—	No presence of soft parts

F: Female; M: Male.

measurements, sex and individual observations made on each specimen; sexually indeterminate specimens were those with empty shells. Two individuals of *A. fontainei* and two *A. loisae* were found in the broken state, lacking soft parts.

Descriptions of Egg Capsules

A female specimen of *A. fontainei* collected in July 2001 was found with 32 egg capsules deposited on its shell, arranged in three rows (Figure 2A). The first row of (12) egg capsules was arranged antero-dorsally on the dorsum of the siphonal canal. The second row of (11) capsules occurred on the dorsum of the last shell whorl, as did the third row of (9) capsules. Each egg capsule was sub-circular (mean length 9.75 mm; mean width 8.89 mm; $n = 32$), biconvex, yellowish in color and opaque. All the capsules had a short peduncle with a very narrow elongated basal portion which was attached to the surface of the shell. Each capsule had a pore on its apical extreme, in a lateral sub terminal position.

The material filling the pore breaks up and dissolves in stages prior to eclosion. The diameter of the pore varied between 0.80 and 2.4 mm (mean 1.57 mm; $n = 29$). Two indentations were notable on the lateral borders of each capsule, which differed in depth and location among the capsules (Figures 11A, B). Numerous capsules contained juvenile snails within a transparent liquid containing tissue remains. A few capsules were stronger and thicker than others, and contained larger amounts of tissue remains and healthy eggs, but no juvenile specimens.

Of the *A. loisae* specimens which carried egg capsules, one had a row of 12 capsules (Figure 2B) of which eight were completely or partially broken. The other *A. loisae* specimen had a row with two partially broken, hatched capsules and the remains of ten peduncles along the length of the shell. The latter egg

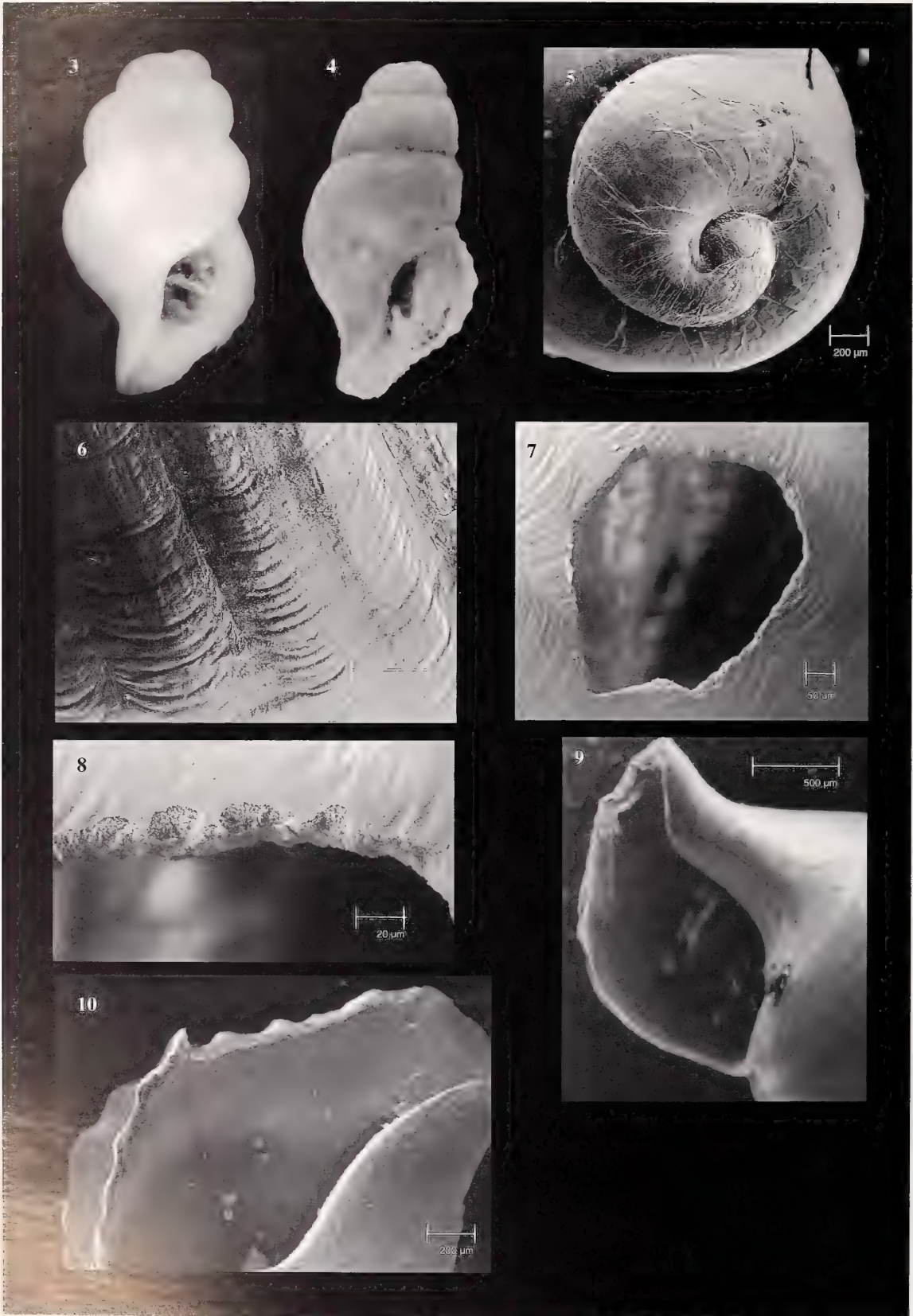
capsules could be differentiated from those of *A. fontainei* by their subcircular oblique form (mean length 8.90 mm; mean width 7.90 mm, $n = 7$), and by the location of the pore in a lateral terminal position (Figure 11B). The diameter of the pore in the *A. loisae* capsules measured 1.9 to 4.0 mm (mean 2.69 mm, $n = 4$). The lateral borders of these capsules were smooth.

Description of the Juveniles

The fifty intracapsular larvae of *A. fontainei* were in an advanced stage of development.

Their shells were thick, well calcified and fusiform, with lengths ranging from 3.12 to 3.25 mm (Figure 3). The protoconch was rounded with 1.5 whorls and was covered with a thin, almost smooth, periostracum, with few folds (Figure 5). The teleconch had three convex, smooth whorls, with initiation of spiral, wide grooves on the penultimate whorl. The last, largest whorl, had a diameter almost equivalent to the preceding ones, and its surface bore spiral, better developed grooves (Figure 6), similar to adult individuals. The shell aperture was elongated with an average length of about 1.57 mm and width of about 0.77 mm. The border of the shell aperture was smooth and sharp (Figure 9). The aperture was bordered by a still developing, short, wide siphonal canal, showing the beginning of formation of a columnar callus. It was of interest to note that one specimen was found to have a shell penetration (Figure 7) on the last whorl of the teleconch.

The two intracapsular juveniles of *A. loisae* were not obtained alive. Their shells, similar to those of *A. fontainei*, were thick and well calcified, with the teleconch composed of three convex whorls. Maximum lengths of these juveniles were 3.52 and 3.84 mm (Figure 4). The shell aperture was elongated, with a length of 2.02 mm and width of 0.99 mm. The border of the aperture lip was undulated due to the presence of



external ribs, in clear contrast to that of *A. fontainei* (Figure 10). The protoconch bore similar characteristics to those of *A. fontainei*, although greater detail was not available due to the eroded condition of the specimens. Table 3 gives the numbers and measurements of egg capsules and juvenile specimens of both species studied.

External Anatomy of Adults (Figures 11C, D)

The study of the external anatomy of *A. fontainei* and *A. loisae* was based on specimens who had been formalin-fixed, and thus the measurements obtained represent partially constricted structures.

From the ventral aspect, both *A. fontainei* and *A. loisae* showed a broad foot which was dark reddish in color, with the lateral border granulose where the propodial groove was observed. The posterior portion of the foot bore a large, horny operculum which was dark brown in color, showing growth rings. The operculum was oval shaped with a pointed tip directed toward the left (Figures 11F, H). In both species the nucleus of the operculum is marginal. The maximum length of the *A. fontainei* operculum was 19.15 mm ($n = 2$) and that of *A. loisae* 22.4 mm ($n = 1$). Operculum is of moderate size (2/3 aperture length), ovate and corneous.

In both species the mantle was observed as a broad sheet with a smooth border, and to be unpigmented. Its left anterior region was extended as a semi tubular, elongated siphon. It was noted that the *A. loisae* siphon was thinner and longer than that of *A. fontainei*.

The heads of both *A. fontainei* and *A. loisae* each had two retractile tentacles. The lateral part of the anterior third of each tentacle bore easily visible pigmented eyespots.

The penis of the male specimens was located above the right tentacle and immediately beneath the mantle edge. The penis of *A. fontainei* was 30.8 mm long; it was relatively thick, with its proximal portion widened to 8.6 mm, representing 27.9% of its total length. The distal end of the penis was thin and pointed (Figures 11C, E). The penis of *A. loisae* (Figures 11D, G) was relatively larger, with a length of 32.6 to 37.5 mm (mean 34.7; $n = 3$). It differed from that of *A. fontainei* in being thicker in proximal and median sections, with

the proximal thickness representing 30% of its' total length. Its' tip was blunt and not pointed as observed in *A. fontainei*.

Both species presented a notable vas deferens as a thick cord running along the right side of the mantle floor. The soft parts of the female specimen of *A. fontainei* were anatomically similar to those of the males, except for the presence of the penis and vas deferens.

DISCUSSION

The findings of the present study extend the range of these species to the Chilean fjord region to 45°21'S. Existing literature does not present reproductive or morphological details, which makes the present study of interest as the specimens were found during a reproductive period.

The presence of egg capsules on the shells of *A. fontainei* and *A. loisae* represent specialized behavior typical of species from deep water habitats with soft bottoms. They probably deposit egg capsules on each other's shells when unable to find other hard substrates suitable for receiving the capsules. This type of adaptation has also been observed in *Chorus giganteus* Lesson, 1829, which live on muddy sand bottoms between 8 and 30 m depth. Here, gregarious reproductive behavior of this species culminates in deposition of egg capsules on the shells of congeners (Gallardo, 1980). The results of the present study have shown differences between the egg capsules of *A. fontainei* and *A. loisae*. The capsules of *A. fontainei* had indented lateral borders not observed on capsules of *A. loisae*, with the form and positions of indentations unique to each capsule. Other important differences between the species studied included the erect position of the egg capsule, and terminal location of the pore in *A. loisae*, versus the inclined position and lateral subterminal location of the pore in *A. fontainei*. These differences between species which belong to same genus have been observed by Gulbin (2000) who describes the morphology and structure of the egg capsules, young and adult specimens of three species of *Pyrulofusus* in the north Pacific and subarctic region. Results showed differences in the shape of egg capsules and in spiral

Figure 3. External anatomy of *A. fontainei* juvenile. 3.52 mm in length.

Figure 4. External anatomy of *A. loisae* juvenile. 3.10 mm in length.

Figure 5. Protoconch of *A. fontainei* juvenile. (SEM).

Figure 6. Grooves on teleconch of *A. fontainei* juvenile. (SEM).

Figure 7. Shell perforation, juvenile *A. fontainei*. (SEM).

Figure 8. Shell perforation from Figure 7, enlarged. (SEM).

Figure 9. Shell aperture, *A. fontainei* juvenile. (SEM).

Figure 10. Shell aperture, *A. loisae* juvenile (SEM).

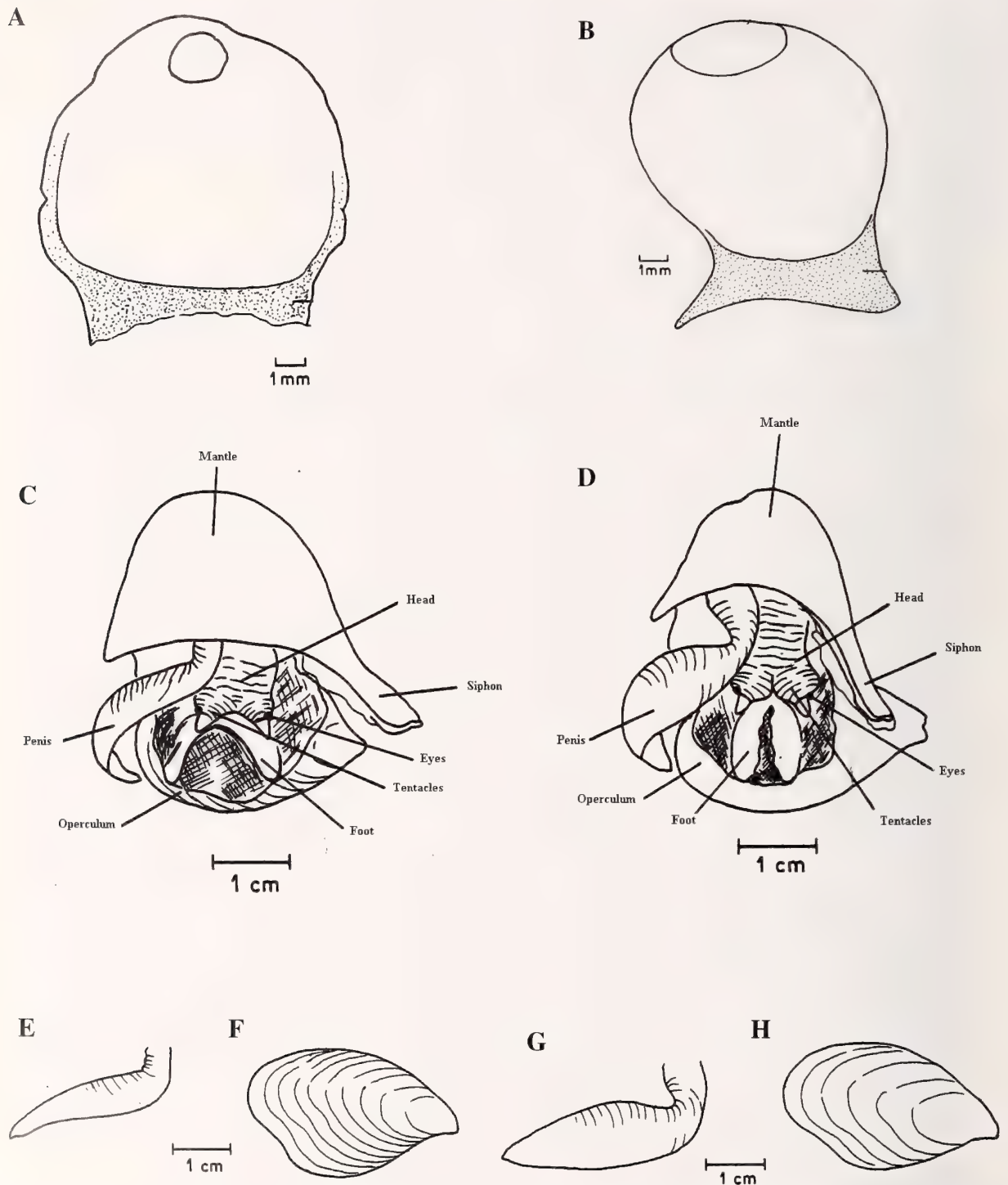


Figure 11. Capsules and external anatomy of adult *A. fontainei* and *A. loisae*. A. Anterior view of an *A. fontainei* egg capsule. B. Anterior view of an *A. loisae* egg capsule. C. Soft parts of *A. fontainei*. D. Soft parts of *A. loisae*. E. Penis of *A. fontainei*. F. Operculum of *A. fontainei*. G. Penis of *A. loisae*. H. Operculum of *A. loisae*.

Table 3

Counts and measurements on egg capsules and juveniles of *A. fontainei* and *A. loisae* obtained during CIMAR Fjord Cruises 7 and 8.

Species	Rows	Egg capsules		Width (mm) (mean \pm SD)	Juveniles	
		Number	Large (mm) (mean \pm SD)		Number/egg capsule (mean \pm SD)	Large (mm) (mean \pm SD)
Cruise CIMAR Fjord 7						
<i>A. fontainei</i>	1	9	9.83 \pm 0.38	8.76 \pm 0.26	6.33 \pm 2.08	3.25 \pm 0.52
	2	11	9.34 \pm 0.33	8.35 \pm 0.23	6.20 \pm 1.48	3.12 \pm 0.28
	3	12	10.04 \pm 0.50	9.48 \pm 0.27	Rest	—
Cruise CIMAR Fjord 8						
<i>A. loisae</i>	1	7	8.90 \pm 0.37	7.90 \pm 0.84	2.0*	3.68 \pm 0.23

* Observation: Juveniles in *A. loisae* were found in an open and semi-broken egg capsule.

sculpture in young specimens in the three species of this genus.

Also, differences observed in the sizes and stages of development of intracapsular juveniles from the three rows of capsules obtained from the female *A. fontainei* suggested that each row may have been produced by a different female. A similar observation was recorded by Gallardo (1981) for capsule deposition by *Chorus giganteus* observed in the laboratory.

The transparent liquid observed within the capsules of *A. fontainei* in which were suspended the juveniles and tissue remains may have contained remnants of nutritive eggs, suggesting that the juveniles of this species may be adapted to lecithotrophic feeding as also observed by Gallardo (1981) for *Chorus giganteus*; West (1983) for the buccinid *Colus stimpsoni* Mörch, 1867 and Martell et al. (2002) in *Buccinum thermophilum*. This phenomenon is thus a broadly distributed developmental strategy among the neogastropods. However, Gulbin (2000) observed in *Pyrulofusus dextris* (Dall) that there is an additional food source, the protein layer of the capsule.

Shell boring is a broadly recognized predatory

strategy among the muricids (Gordillo & Amuchastegui, 1998), both in early stages of development and in adults. Cannibalism among juveniles as young as 10 days in age has been observed in *Chorus giganteus* when other naturally occurring food is unavailable (Gonzalez & Gallardo, 1999). Similar behaviour between encapsulated individuals may explain our observation of shell penetration seen in *A. fontainei* (Figure 7), as well as the apparent radular attack observed on shell borders of other larvae in the capsule (Figure 8).

The form of the penis shows large variation among molluscs, and is the anatomical characteristic of most importance among the Littorinidae (Reid, 1986). Observations on individuals of the presently studied species of *Aeneator* indicate there is no external sexual dimorphism between shells of adult males and females, but sexual dimorphism is notable from the soft parts, when considering the presence of a well developed penis in the males. In this study the two species were readily separated based on the longer and basally thicker penis in the male *A. loisae*, compared with that of *A. fontainei*.

Table 4

Comparison between numbers and size of juveniles and adults of gastropods with direct development.

Species	Number juveniles/capsules	Size juveniles (mm)		Length adults (mm)	Authors
		Range	Mean		
<i>Adelomelon brasiliana</i>	9–33	—	~10.0	160	Nuñez y Narosky (1997)
<i>Zidona dufresnei</i>	2–6	—	18.0	207	Nuñez y Narosky (1997)
<i>Acanthina monodon</i>	10–122	0.83–1.30		65	(Gallardo, 1979)
<i>Trophon geversianus</i>	5–45	—	3.0	82	Gallardo & González (1994)
<i>Trophon plicatus</i>	3–38	1.8–3.3	—	50.0	Penchaszadeh, 1976 Pastorino, 2005
<i>Aeneator fontanei</i>	2–8	3.12–3.25	—	103–128	Present study
<i>Aeneator loisae</i>	2*	3.52–3.84	—	105–128	Present study

* Observation: Juveniles in *A. loisae* were found in an open and semi-broken egg capsule.

The large size of the juveniles (Table 4) produced by species with holobenthic development may be an adaptation to intracapsular development. The additional food source by nurse eggs (Gallardo & Gonzalez, 1994), protein layer capsules (Gulbin, 2000) and intracapsular cannibalism (present work) may enable the individuals to hatch at a large size immediately suited for survival in the adult habitat.

Finally, all species mentioned have in common a high latitude distribution and direct embryonic development. However, species vary in sizes and numbers of their eggs and in the range of juvenile size and/or capsule number, so it is difficult to generalize about species with direct development.

Literature existing prior to the present study classified *A. fontainei* and *A. loisae* strictly on the basis of shell morphology. Our data on reproductive characteristics, such as oviposition, egg capsule structure and larval morphology, and anatomical observations of adult soft parts, now broadens their taxonomic characterization.

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Two New Species of Conoidean Gastropods (Gastropoda: Conoidea) from the Northern South China Sea

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Abstract. Two new species from the northern part of the South China Sea of the families Conidae and Turridae (Neogastropoda: Conoidea) are described: *Tritonoturris concinnus* sp. nov. and *Ptychobela salebra* sp. nov. *Tritonoturris concinnus* differs from the closely allied species *T. macandrewi* (E. A. Smith, 1882), by having fewer and stronger axial ribs and a more convex body whorl; *Ptychobela salebra* differs from its closely allied species *P. flavidula* (Lamarck, 1822), by having more numerous and sharper spiral cords, much more convex whorls with a more angled slope, and a coarser shell surface.

INTRODUCTION

The Conoidea is a highly diverse group of gastropods, with over 4000 species having been described in the family Turridae alone (Powell, 1964, 1966; McLean, 1971; Wells, 1990; Kilburn, 1983). Unfortunately, the Turrid fauna from the China seas is still poorly known (MA, 1983, 2004). Recently, when we sorted the turrid collection of the Marine Biological Museum of the Chinese Academy of Sciences (MBMCAS, Qingdao) in the Institute of Oceanology, Chinese Academy of Sciences (IOCAS, Qingdao), two forms were encountered which could not be assigned to any described species, and are described as new species in the present paper.

The material were collected by investigations carried out since the 1950s, including the “National Comprehensive Oceanography Survey” (NCOS, 1958–1960) carried out by the Chinese government, “China-Vietnam marine resource investigation cooperative of Beibu Gulf (= the Gulf of Tonkin)” (1959–1962), “The resource investigation of coastal and shallow waters of Shandong Province,” “The comprehensive resource investigation of the islands of China,” “China-Germany marine biota cooperative investigations of Hainan Island, China” (1990–1992), by intertidal zone collection or trawling.

All the material is deposited in the MBMCAS, Qingdao.

Abbreviations in the text are as follows:

AT—Agassiz trawl

BT—beam trawl

CN—preliminary registration number of collection

IOCAS—Institute of Oceanology, Chinese Academy of Science

MBMCAS—Marine Biological Museum of the Chinese Academy of Sciences in the Institute of Oceanology, Chinese Academy of Sciences

RN—museum registration number

SCS—the South China Sea.

spm—specimen.

SYSTEMATICS

The taxonomic system is based on the proposals of (Taylor et al., 1993).

Family Conidae Fleming, 1822

Subfamily Raphitominae Bellardi, 1875
(= Daphnellinae Casey, 1904)

Genus *Tritonoturris* Dall, 1924

Tritonoturris Dall, 1924, p. 88. Type species (o.d.)
Clathurella robillardi “Barchy, 1869” = H. Adams, 1869

Tritonoturris concinnus sp. nov.

(Figures 1–4, 5, 6)

Type material: Holotype, RN MBM081112, SCS, 21°00'N, 114°00'E, CN S79B-50, 78 m, Apr. 10, 1959, AT, collector Shaozong WU, MBMCAS.

Paratype: RN MBM081113, SCS, 22°00'N, 116°00'E, CN S227B-43, silty mud, 84 m, Apr. 22, 1960, AT, collector Jingzuo QU, MBMCAS.

Diagnosis: Shell of medium size, 12.2–16.9 mm in height, fusiform, brownish-grey in color. Protoconch

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Figures 1-6. *Tritonoturris concinnus* sp. nov. 1-2, shell of holotype; 3-4, shell of paratype; 5-6 protoconch of paratype. Scale = 50 mm (Figs. 1-4); 200 μ m (Figs. 5, 6).

Table 1
Measurements of *Tritonoturris concinnus* sp. nov.

	RN	Length (mm)	Width (mm)	Aperture (mm)	W/L	A/L
Holotype	MBM081112	16.9	6.9	8.1	0.41	0.48
Paratype	MBM081113	12.2	6.1	6.5	0.5	0.53

multispiral, of about 2.5 whorls. Spire tall, whorls about 7, convex; body whorl strongly convex. Suture deeply impressed. Shell sculptured with numerous strong spiral threads and regular axial ribs, aperture elongate-ovate, columella smooth. Anal sinus relatively shallow, U-shaped. Siphonal canal long, deep and wide.

Description of holotype: Shell of medium size, 16.9 mm in height, fusiform. Protoconch multispiral, of about 2.5 whorls; protoconch I of about 0.5 whorls with very weak spiral sculpture, protoconch II of about 2 whorls sculptured with diagonally cancellated ribs. Spire tall; whorls about 7, convex; body whorl strongly convex. Suture distinct, deeply impressed. Shell sculptured with numerous strong spiral ribs and strong axial ribs. Axial ribs regularly arranged on spire whorls, of about 7 ribs per whorl, and forming a continuous line on successive whorls; 14 ribs on body whorl, not very regular. Primary spiral ribs 6 on penultimate whorl, and about 21 on body whorl; there are also fine secondary spiral threads between primary spiral ribs. Aperture elongate-ovate, widely open; columella smooth. Anal sinus relatively shallow, U-shaped, just below suture. Siphonal canal long, deep and wide, anterior tip of shell notched. Shell brownish-grey in color.

Measurements: See Table 1.

Distribution: Known only from the South China Sea, at the depths of 78–84 m.

Etymology: “concinnus,” Latin: well-arranged, referring to the shell well sculptured with regular axial ribs.

Remarks: Powell (1966) also reported seven characteristic species of genus *Tritonoturris*, and this new species can be separated from the other species on shell outline features and sculpture. The new species is similar to *Tritonoturris macandrewi* (E. A. Smith, 1882), but can be easily distinguished from the latter by having fewer and stronger axial ribs, and a more convex body whorl.

Family Turridae H. & A. Adams, 1853

Subfamily Crassispirinae Morrison, 1966

Genus *Ptychobela* Thiele, 1925

Ptychobela Thiele, 1925, p. 181. Type (o. d.) *Pleurotoma crenularis* Lamarck, 1816.

Ptychobela salebra sp. nov. (Figures 7–9)

Drillia perculathrata Eisenberg J. M., 1981: 150, pl. 132, fig. 13. (evidently a misspelling for *perclathrata*, *nomen nudum*).

Inquisitor perculathrata Chang & Wu, W., 2000, p. 13–26, figs. 6a–b;

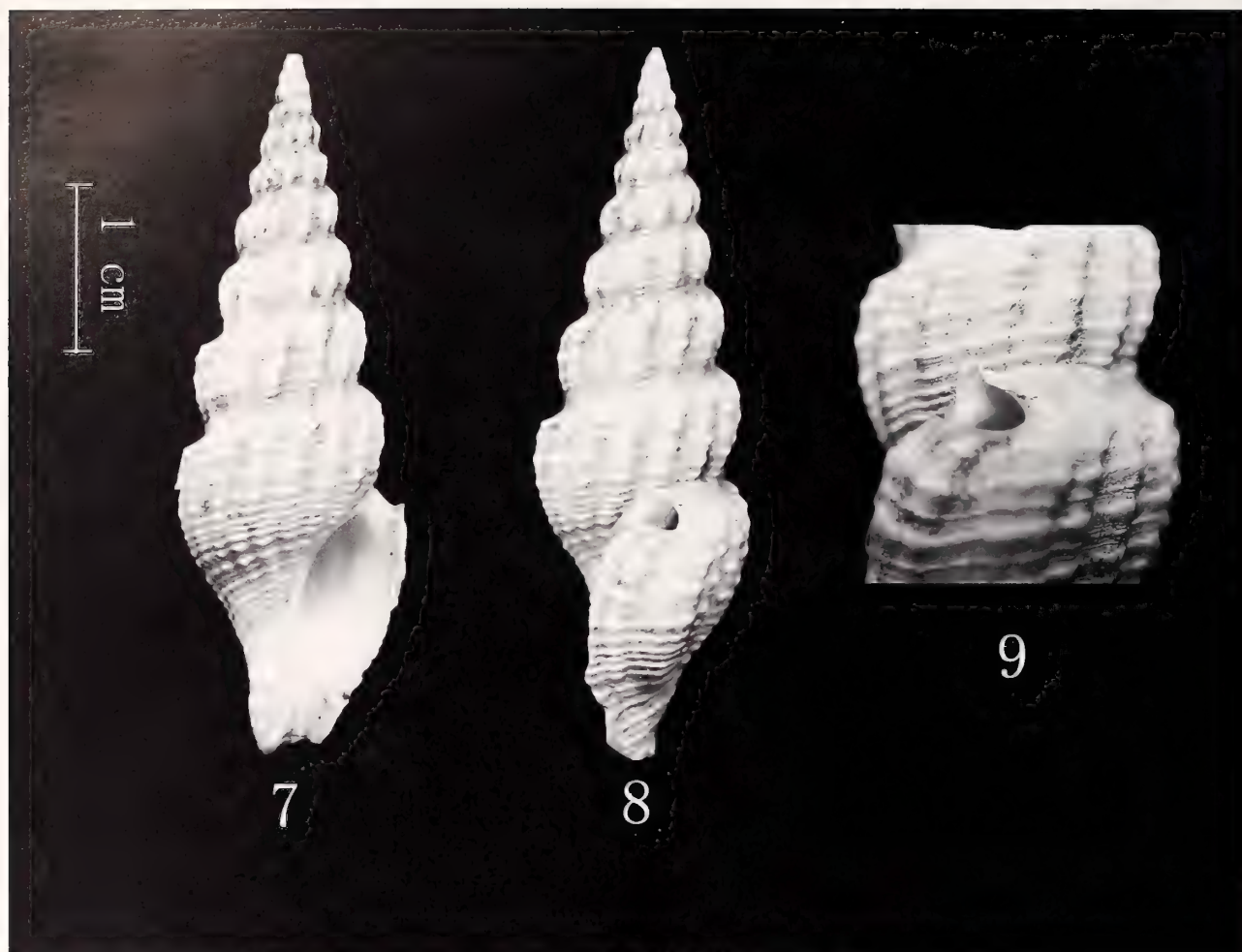
Inquisitor perclathrata Tucker, J. K., 2004: 746 (*nomen nudum*).

Type material: Holotype, RN MBM081114, SCS, 18°15'N, 111°00'E, 170 m, silty mud, Jan. 26, 1959, collector Yongliang WANG, MBMCAS.

Paratypes: 1 spm, RN MBM081115, SCS, 21°45'N, 116°30'E, CN S156B-13, 93.7 m, silty mud, Nov. 20, 1959, AT, collector Wei-quan ZHANG & Shaozong WU, MBMCAS; RN MBM081116, 1 spm, SCS, 22°00'N, 115°30'E, CN S155-B-31, 78 m, silty mud, Dec. 20, 1959, AT, collector Wei-quan ZHANG & Shaozong WU, MBMCAS; RN MBM081117, 1 spm, SCS, 20°30'N, 112°30'E, CN K125B-69, 78 m, muddy sand, Feb. 9, 1960, AT, MBMCAS; RN MBM081118, 1 spm, SCS, 20°00'N, 113°00'E, CN SIII20B-60, 105.3 m, sandy mud, Jul. 14, 1959, AT, collector Wei-quan ZHANG, MBMCAS; RN MBM081119, 1 spm, CN Q115B-11, SCS, 22°00'N, 116°00'E, 88 m, fine sandy mud, Jan. 9, 1960, AT, MBMCAS; RN MBM081120, 1 spm, SCS, 22°00'N, 116°00'E, CN S161B-23, 85 m, fine sand, Oct. 23 1959, AT, collector Wei-quan ZHANG & Shaozong WU, MBMCAS.

Diagnosis: Shell of medium size for genus, 23.0 to 42.3 mm in height, claviform, solid, with a high spire. Whorls obviously convex, about 10, angled at shoulder. Suture channeled, subsutural slope very narrow, concave. Shell sculptured with sharp oblique axial folds and spiral cords, the spiral cords almost equally developed on axial folds and in interstices. Aperture elongate-oval, relatively narrow; outer lip margin thin. Anal sinus relatively deep, U-shaped. Canal moderately short and straight.

Description of holotype: Shell of medium size, 42.3 mm in height, claviform. Spire high, whorls about 10, strongly convex. Suture shallow and wavy. Axial folds strong and sharp, slightly oblique, crossed by strong spiral cords, forming a coarse surface. Subsutural slope narrow and concave. There are about 18 axial folds on body whorl, 15 on penultimate; the next to last axial fold becoming a varix behind outer lip margin. There



Figures 7-9. *Ptychobela salebra* sp. nov., shell of holotype. Scale = 1 cm (Figs. 7-9).

are about 23 spiral cords on body whorl, 6 on the penultimate, and finer secondary spiral lines between primary spiral cords. Aperture elongate-oval, outer lip thin, with indented margin. Anal sinus on subsutural slope, deep, U-shaped. Canal relatively long, notched and recurved. Shell uniformly brownish-yellow.

Measurements: See Table 2.

Distribution: Japan and the South China Sea, 50 to 170 m.

Etymology: "salebra," Latin; roughness, referring to the coarse sculpture of the shell.

Remarks: *Ptychobela salebra* sp. nov. is close to *Ptychobela flavidula* (Lamarck, 1822). It differs from

Table 2
Measurements of *Ptychobela salebra* sp. nov.

	RN	Length (mm)	Width (mm)	Aperture (mm)	W/L	A/L
Holotype	MBM081114	42.3	14.3	18.2	0.34	0.43
Paratype	MBM081115	26.8	9.9	12.7	0.37	0.47
	MBM081116	23.0	8.6	10.2	0.37	0.44
	MBM081117	28.5	9.5	12.5	0.33	0.43
	MBM081118	41.3	13.6	19.3	0.33	0.47
	MBM081119	38.5	12.1	17.5	0.31	0.45
	MBM081120	33.3	11.5	16.2	0.34	0.45

the latter by having more numerous and sharper spiral cords, and much more convex whorls with a more angled slope, and a coarser surface than the latter. Although *Ptychobela* is characterized by a very high variability, after a careful examination of a large series of specimens, we can easily separate this species from the typical form of *Ptychobela flavidula* (the holotype figured by Wells, 1994: 94, pl. 5, figs. 7–8).

Eisenberg (1981) reported this species as *Drillia perculathrata* from Japan and Chang & Wu (2000) reported it as *Inquisitor perculathrata* from Taiwan, China (which is evidently a misspelling for *perclathrata*). Tucker (2004) briefly reviewed the species, he thought that *I. perclathrata* was credited to Kuroda, MS in Azuma and to Kuroda in Eisenberg, but is a *nomen nudum* in both Azuma and Eisenberg, and unavailable in Chang & Wu. There is no statement of intention to propose a new name. So, we reported this species as new to science, and tentatively placed it in the Genus *Ptychobela*.

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A New Gigantic *Nucinella* (Bivalvia: Solemyoida) from the Cretaceous Cold-seep Deposit in Hokkaido, Northern Japan

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Abstract. *Nucinella gigantea*, sp. nov. is described from the Campanian cold-seep deposits in Hokkaido, northern Japan. This species is characterized by its gigantic size within the genus and by its radiating interior striation. Its morphological features, associated fauna, lithofacies and carbon isotope suggest that *N. gigantea* lived in the bathyal cold-seep site, and depended on chemosymbiosis. In addition, this new species is the oldest known *Nucinella* invader of deep cold-seep environments.

INTRODUCTION

Species of the genus *Nucinella* Wood, 1851 are rare bivalves ranging from shallow waters to lower bathyal depths (La Perna, 2005, Table 1; Okutani & Iwasaki, 2003). Based on the soft-part anatomy and shell structure, the genus was transferred from Arcoida of Pteriomorpha to Solemyoida of Protobranchia (Allen & Sanders, 1969; Waller, 1978).

In Japan, seven species of Recent and fossil nucinellids have been described: *Nucinella kanekoi* Matsukuma, Okutani & Tsuchi, 1982, *N. viridis* Matsukuma, Okutani & Tsuchi, 1982, *N. surugana* Matsukuma, Okutani & Tsuchi, 1982, *Huxleya sulcata* A. Adams, 1860, *H. decussata* A. Adams, 1862, *H. ochiaiensis* (Chinzei, 1959) and *H. cavernicola* Hayami & Kase, 1993. *H. sulcata* and the extinct *H. ochiaiensis* have been recorded from the Plio-Pleistocene formations in the Northeast Honshu and Kanto district of central Honshu (Baba, 1990) whereas *N. kanekoi* is also known from the Pliocene Takanabe Formation of the Miyazaki Group in Miyazaki Prefecture, southern Kyushu (Matsukuma et al., 1982).

A new gigantic species of *Nucinella* was collected from the Cretaceous cold-seep site in Nakagawa Town in northern Hokkaido. This is the second record of *Nucinella* from cold seep sites, after the Recent species *N. viridis* (Okutani & Iwasaki, 2003; Sasaki et al.,

2005). Therefore, this is the oldest record of *Nucinella* in Japan and the first record from a fossil cold-seep site.

MATERIALS AND METHODS

Fossil specimens of the present new species were collected from the Campanian Omagari Formation of Upper Yezo Group (Takahashi et al., 2003) at about 400 m downstream of Abeshinai River from the junction with Tanno-sawa Creek (Figure 1). The name coined for the locality is Yasukawa site (Jenkins, 2006). Four carbonate bodies, each larger than 50 cm in diameter, here named A to D, were identified at the Yasukawa site. We examined the largest carbonate body and surrounding sandy siltstone (Carbonate body A, 1 m × 2 m) which yields some small bivalves, including the new species of *Nucinella* and gastropods (Jenkins, 2006). The new species of *Nucinella* was also collected from mudstone overlying the cemented sandstone, and mudstone located laterally 5 m away but on nearly the same horizon as Carbonate body A (the name coined for the locality is Yasukawa Peripheral Site; YPS). All fossil specimens are housed at the University Museum, the University of Tokyo (UMUT).

According to Jenkins et al. (2007), the carbonate body can be divided into upper and lower parts (40 cm and 60 cm thick, respectively). The lower part is composed mainly of fractured micritic limestone. The

Table 1

Associated species with a new species of *Nucinella*.

Species
<i>Serradonta</i> sp.
Ataphridae gen. et sp. indet.
Abyssochrysidae gen. et sp. indet.
<i>Acharax cretacea</i> Kanie and Nishida
<i>Leionucula formosa</i> (Nagao)
<i>Acila</i> (<i>Truncacila</i>) <i>hokkaidoensis</i> (Nagao)
<i>Nuculana</i> (<i>Ezonuculana</i>) <i>mactraeformis</i> Nagao
<i>Propeamussium yubarensis</i> (Yabe and Nagao)
<i>Myrtea ezoensis</i> (Nagao)
<i>M.</i> ? sp.
<i>Miltha</i> sp.
<i>Thyasira</i> sp.
<i>Fissidentalium</i> cf. <i>otatunei</i> (Nagao)

upper part is mainly composed of cemented sandstone (i.e., grainstone) with cements of radiaxial bladed calcite and sparry calcite. Isotopic composition of early cemented phases, i.e., micrite and radiaxial bladed calcite, ranges from -43.5 to 37.7% for $\delta^{13}\text{C}$ (vs. PDB) and from -2.7 to -0.4% for $\delta^{18}\text{O}$ (vs. PDB). These oxygen isotope values closely resemble the values from Campanian shells of benthic animals examined from the outer shelf to upper slope settings in the north-western Pacific (Moriya et al., 2003). The negative $\delta^{13}\text{C}$ values of the early precipitated carbonates indicate that their carbon was derived from biogenic and/or thermogenic methane (Peckmann & Thiel, 2004). This

fact, as well as the variable sulphide sulphur isotopic compositions, high carbonate contents, and *in situ* fractures in the carbonates, strongly suggest that this locality was a methane-seep site (Jenkins, 2006).

On the measurement of shells, Matsukuma et al. (1982) proposed to measure "shell length" along the antero-posterior axis passing through the supposed locations of mouth and anus. However, most authors measured shell length as parallel to hinge axis. We use this traditional method to measure the shell length and height, as claimed by La Perna (2005) for comparing the new species with other ones. La Perna (2005) measured height as the beak-ventral distance and length as the antero-posterior one at right angle to height.

SYSTEMATICS

Family Manzanellidae Chronic, 1952

Remarks: This family includes *Manzanella* Girty, 1909 (Early Permian), *Nucinella* Wood, 1851 (Early Jurassic to Recent) and *Huxleya* A. Adams, 1860 (Pliocene to Recent). Assignment of these genera to a single family (Manzaniellidae) or two families (Manzaniellidae and Nucinelidae Vokes, 1956) is controversial. Habe (1977) and Pojeta (1988) separated Nucinelidae including some living species from the extinct Manzanellidae. Vokes (1956) considered *Manzanella* is included in the same family to *Nucinella* and *Huxleya* when he summarized supraspecific group of Nucinelidae and all species of *Nucinella*. Then, he regarded Nucinelidae as a junior synonym of Manzanellidae (Vokes, 1980). In his cladistic work on bivalves, Waller (1990, 1998) shows high-rank segregation of Nucinelidae and Manzanellidae from other solemyoids and consequently combined two families. Thus, we follow the conclusions of Vokes (1980) and Waller (1990, 1998).

Genus *Nucinella* Wood, 1851

Nucinella gigantea Amano, Jenkins and Hikida,
sp. nov.

(Figures 2–7)

Diagnosis: A gigantic *Nucinella* having nuculid shape and with many radiating interior striae and narrow flat area below dentition.

Holotype: Length—18.4 mm, height—18.8 mm, width—10.4 mm, both valves, UMUT MM29245; Carbonate body A.

Paratypes: Length—8.9 mm, height—9.8 mm, width—4.9 mm, both valves, UMUT MM29246; length—7.9 mm, height—7.9 mm, width—4.2 mm, both valves, UMUT MM29247; length—6.5 mm, height—6.9 mm,

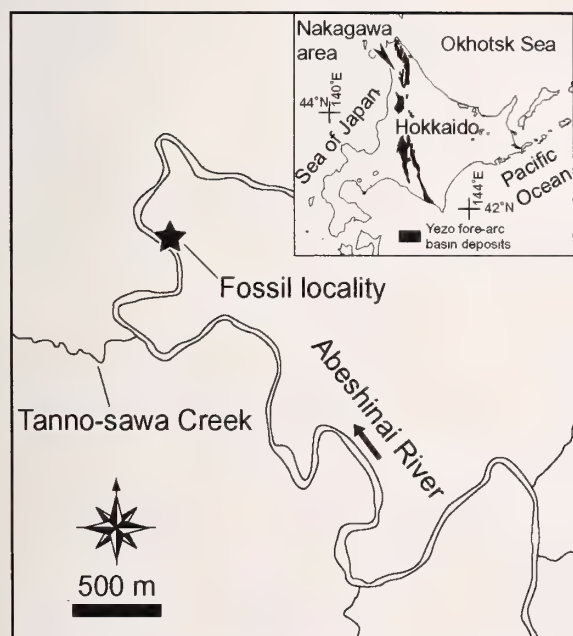
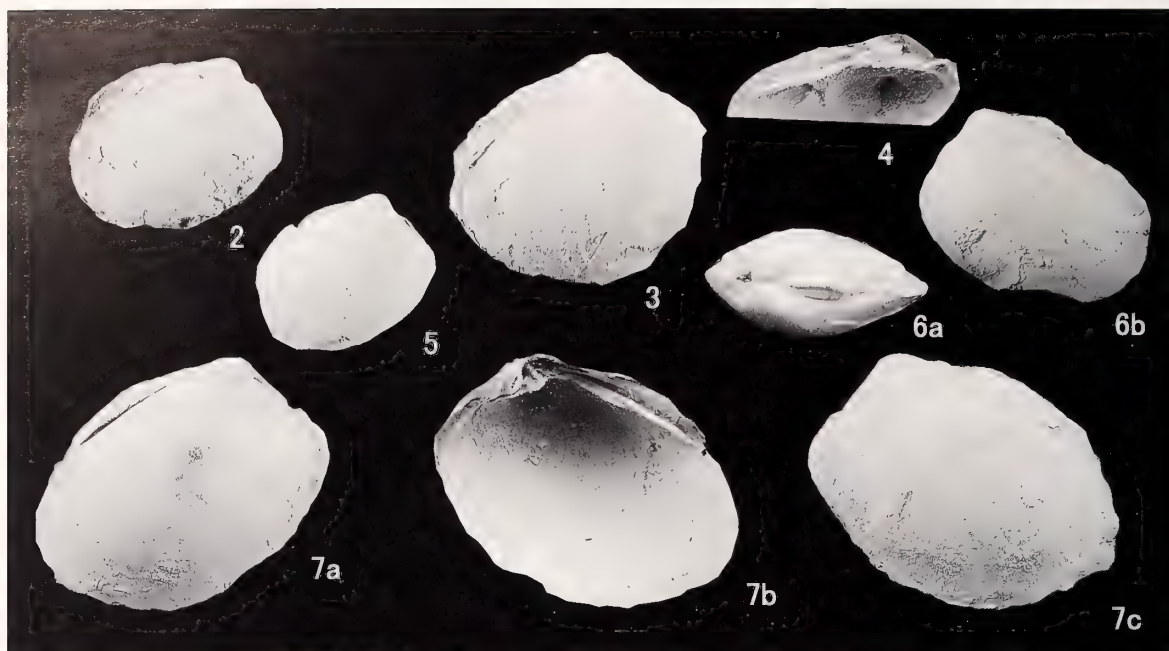


Figure 1. Locality of a new species of *Nucinella*.



Figures 2–7. *Nucinella gigantea* Amano, Jenkins & Hikida. Figure 2, Paratype, length = 7.9 mm, UMUT MM29247. Figure 3, Paratype, length = 13.2 mm, UMUT MM29250. Figure 4, Paratype, length = 12.1 mm, UMUT MM29249. Figure 5, Paratype, length = 6.5 mm, UMUT MM29248. Figures 6a–b, Paratype, length = 8.9 mm, UMUT MM29246. Figures 7a–c, Holotype, length = 18.4 mm, UMUT MM29245; Figure 7b, rubber cast of Holotype.

width—3.1 mm, both valves, UMUT MM29248; length—12.1 mm, height—5.4 mm (deformed), right valve, UMUT MM29249; YPS: Length—13.2 mm, height—11.2 mm, left valve, UMUT MM29250; Carbonate body A.

Type locality: 400 m downstream of Abeshinai River from the junction with Tanno-sawa Creek, Nakagawa Town, Hokkaido (44°40'27"N, 142°1'45"E); Omagari Formation.

Stratigraphic and geographic distribution: Late Cretaceous (Campanian), Omagari Formation; known only from the type locality.

Description: Shell gigantic in size, thin-walled, moderately inflated, nuculiform, equivalve, inequilateral. Umbo projecting above dorsal margin, opisthogryate, posteriorly situated at about one-third of shell length. Antero-dorsal margin long, broadly arcuated, grading into rounded anterior margin; antero-ventral margin well rounded; postero-ventral margin nearly straight; postero-dorsal margin short, steeply sloping, making right angle with postero-ventral margin. Surface smooth, except for very weak growth lines. Hinge plate not so wide, consisting of subumbonal taxodont teeth and anterior lateral tooth. In right valve; two central teeth large, but thin; more than two anterior teeth small; two posterior teeth small, chevron shaped, parallel to hinge, just behind central teeth; anterior

lateral tooth long and elevated. In left valve; one central tooth strong; more than five posterior teeth small; three anterior teeth parallel to hinge; one anterior lateral tooth strong and long. Ligament pit wide and deep, immediately situated at posterior of beak, occupying postero-dorsal margin. Monomyarian condition advanced, anterior adductor muscle scar large and ovate. Inner surface with very fine radial striations. Pallial line entire.

Comparison: Most species of fossil and Recent *Nucinella* have very small adult shells (length = about 1 to 3 mm). Exceptionally, three Recent species attaining and even exceeding 1 cm in shell length are known from the deep sea: *Nucinella maxima* (Thiele & Jackel, 1931) from Zanzibar Channel, eastern Africa (463 m deep), *N. viridis* Matsukuma, Okutani & Tsuchi, 1982 from off Nojimazaki, central Honshu (2630–3581 m deep) and *N. boucheti* La Perna, 2005 from Bondoc Peninsula, Philippines (1580–1610 m deep). *N. gigantea* is a member of such a large shelled species group. Among them, *N. boucheti* closely resembles *N. gigantea* in its large shell size (length = 25 mm), nuculiform outline and fine radiating interior striation. However, *N. boucheti* differs from *N. gigantea* in having a wide triangular flat area below dentition and more numerous teeth (13 in the holotype). *N. maxima* is another species similar to *N. gigantea*, with two vertical central teeth, similar number of teeth (6 or 7) and interior

striation. Smaller size ($L = 12.5$ mm) and the obtusely rounded posterior corner of *N. maxima* enable us to separate this species from *N. gigantea*. *N. viridis* differs from *N. gigantea* by having a smaller shell ($L < 10.4$ mm), fewer teeth (5) and obtusely rounded posterior corner.

Two other species of *Nucinella* have been recorded from Cretaceous deposits: *N. glabrata* Stoliczka, 1871 from the Ootatoor Group in South India and *N. sohli* Pojeta, 1988 from the Blufftown Formation in Georgia, USA (Vokes, 1956; Pojeta, 1988). However, their small size (length = 3.1 mm in *N. glabrata* and length = 2 mm in *N. sohli*) easily distinguishes them from *N. gigantea*. Although the inner surface of *N. glabrata* is unknown in detail, *N. sohli* distinctly lacks the radiating interior striation.

Associated species and paleoenvironment: At the type locality, this new species was collected from the Carbonate body A, and its surrounding sandy siltstone and mudstone, and YPS together with many taxodont bivalves, lucinids and thyasirids (Table 1). Among them, *Acharax cretacea* Kanie & Nishida, 2000, *Myrtea ezoensis* (Nagao, 1938), *Miltha* sp. and *Thyasira* sp. might be chemosymbiotic bivalves. In contrast, *Leionucula formosa* (Nagao, 1930), *Acila* (*Truncacila*) *hokkaidoensis* Nagao, 1932, *Nuculana* (*Ezonuculana*) *mactraeformis* Nagao, 1932 might be deposit feeders. *Propeamusium yubarens* (Yabe & Nagao, 1928) is thought to be a carnivore (Hickman, 1984). The high ratio (0.5) of protobranch bivalves to total bivalve species shows a habitat deeper than the lower sublittoral zone (Amano et al., 1987; Amano & Nonaka, 2001; Amano, 2003). On the other hand, the Recent records of small associated gastropod *Serradonta* Okutani, Tsuchida & Fujikura, 1992 is restricted to bathyal depth in the Pacific (Warén & Bouchet, 2001; Sasaki et al., 2005). Judging from these associated fauna and lithology, this new species lived at around the bathyal cold-seep site.

Etymology: This species named after its size.

DISCUSSION

La Perna (2005) suggested that the large body size of *N. boucheti*, together with deep sea colonization, may be an expression of the evolutionary diversification of *Nucinella*. In fact, other than *N. maxima* living in the upper bathyal zone, large species of *Nucinella* now live in the middle to lower bathyal depth while most small species live in the upper sublittoral to upper bathyal zones (La Perna, 2005). However, it is difficult to explain how low nutrient conditions of the deep sea could sustain such large species.

Taylor & Glover (2000) estimated chemosymbiosis of fossil Lucinidae, partly based on the study of

symbiosis-associated morphological features. Reid (1990) listed the genera possessing sulphide-oxidizing bacteria including *Solemya* Lamarck, 1818, *Acharax* Dall, 1908, *Calyptogena* Dall, 1891, *Bathymodiolus* Kenk & Wilson, 1985, *Lucinoma* Dall, 1901, *Parvilucina* Dall, 1901, *Anodontia* Link, 1807, *Codakia* Scopoli, 1777, *Linga* De Gregorio, 1884, *Myrtea* Turton, 1822, *Thyasira* Lamarck, 1818 and so on. Although the exact reason is unknown, most species of these genera have radiating interior striation. The large-sized *N. boucheti*, *N. maxima* and *N. gigantea* have such striation while small-sized *N. serrei* Lamy, 1912 and *N. adamsi* (Dall, 1889) lack this feature (Lyle Campbell, personal communication). Moreover, Reid (1990) inferred that the large species *N. maxima* may harbor sulphide-oxidizing bacteria based on its gutless condition pointed out by Kuznetsov & Schileiko (1984). In contrast, Allen & Sanders (1969) described a normal gut in the small species, *N. serrei*. In addition, as above noted, another large species, *N. viridis*, has been found at the cold seep sites (Okutani & Iwasaki, 2003; Sasaki et al., 2005). Furthermore, all solemyid species live in symbiosis with sulfur-oxidizing bacteria (Fisher, 1990). The solemyid bivalves first entered cold-seep conditions in the Carboniferous (Peckmann et al., 2001) and are widely distributed in post-Carboniferous hot-vent and cold-seep environments (Campbell, 2006). Molecular phylogeny of the endosymbiotic bacteria suggest that the solemyid bivalves harbored the bacteria in ancient times (Imhoff et al., 2003). Based on these criteria and on the ecology of related species, we believe that the large size of *Nucinella* may be attributed to chemosymbiosis. Conversely, small size of fossil and living species of *Nucinella* may indicate deposit feeding, as in other protobranchs and shallow water dwellers. Of course, to settle this hypothesis, it is necessary to make a direct examination of the symbiosis on the Recent large *Nucinella*. *N. gigantea* appears to be the earliest *Nucinella* to invade the cold seeps, presumably because of its chemosymbiosis.

When he discussed paleobiogeographic history of European nucinellids, La Perna (2004) pointed out that the fossil species, other than the Pleistocene *N. seguenzae* (Dall, 1898), lived in shelf environment and then later migrated to deeper water. The oldest record of *Nucinella* is from the early Jurassic of Europe (Vokes, 1956). Based on this record, La Perna (2004) also postulated that this genus originated in the western Tethys region. Our new data show that the migration from the western Tethys to the eastern part occurred in pre-Cretaceous time and the invasion to the deep sea dates back to the Campanian.

In the northeastern Pacific region, a small species, *N. oregona* (Vokes, 1956) has been recorded from the Nestucca Formation in Oregon whose age is late middle Eocene (Prothero, 2001). From the middle

Eocene Cook Mountain Formation, *N. alleni* Vokes, 1966 was found in the eastern coast of America. By our data, it is possible to infer two migration routes of the northeastern Pacific *Nucinella*. As the Central American Seaway was present at that time (e.g. Coates & Obando, 1996), it was possible for *Nucinella* to migrate from the Atlantic to the Pacific side as did the venerid genus *Securella* Parker, 1949 (Vermeij, 2001). Another possibility is the eastward trans-Pacific migration as shown in some cold-water mollusks (Amano, 2005). The current through the Central American Seaway in the Eocene (Iturralde-Vinent, 2003) supports the former alternative. For settling this problem, much more fossil data of *Nucinella* are needed especially from the North Pacific region.

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Field Observations on the Feeding of the Nudibranch *Gymnodoris* spp. in Japan

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Abstract. Here, we report field observations of the diets of some *Gymnodoris* species (Nudibranchia: Opisthobranchia) inhabiting warm waters in the vicinity of Japan. Some *Gymnodoris* species appeared to feed exclusively on a single species: *G. ceylonica* fed on *Nakamigawaia* sp.; *G. okinawae* on *Elysia* sp.; *G. striata* on *Elysia ornata*; and an undescribed *Gymnodoris* sp. fed on *Glossodoris cincta*. In contrast, other *Gymnodoris* species fed on multiple species: *G. citrina* fed on *G. okinawae* and eggs of nudibranchs; *G. inornata* fed on *G. rubropapulosa* and *Dendrodoris fumata*; and *G. rubropapulosa* fed on *Chromodoris annae*, *C. strigata*, *Chromodoris* sp., *Hypselodoris festiva*, and *Mexichromis multituberculata*.

INTRODUCTION

Except for some species of Cephalaspidea, Sacoglossa, and Anaspidea, opisthobranch mollusks are carnivorous. Each carnivorous opisthobranch feeds on particular prey items, e.g., sponges, hydroids, bryozoans, or ascidians. Some carnivorous opisthobranchs prey on other opisthobranchs and their eggs (see Behrens, 2005). These opisthobranch-feeding opisthobranchs include *Chelidonura* (Gosliner et al., 1996), *Navanax* (Paine, 1963), *Philinopsis* (Rudman, 1972), *Pleurobranchaea* (Battle & Nybakken, 1998), *Gymnodoris* (Kay & Young, 1969), *Roboastrea* (Farmer, 1978), *Melibe* (Kay, 1979), and *Godiva* (Gosliner, 1987b). *Gymnodoris* species usually feed on opisthobranchs and/or their eggs, except for *Gymnodoris nigricolor*, which apparently lives on some species of goby (Osumi & Yamasu, 1994), such as *Amblyeleotris japonica* (Williams & Williams, 1986), by grasping the fins using their buccal apparatus.

Few studies have reported on the diets of other *Gymnodoris* species, particularly in their natural habitats. To date, diets have been reported for nine *Gymnodoris* species (Table 1). Some *Gymnodoris* species appear to feed exclusively on a single species, whereas others feed on multiple species. However, there is considerable doubt whether animals in the laboratory show their natural food habits. Therefore, data on the feeding behavior of *Gymnodoris* species should be collected in their natural habitat. To this end, we examined diets of some *Gymnodoris* species inhabiting warm waters in the vicinity of Japan.

MATERIALS AND METHODS

From 2000 to 2006, *Gymnodoris* species feeding on prey in their natural habitats were directly observed by SCUBA diving at Hachijo-jima Island, Tokyo (33°6' N, 139°46' E), Ohomi-jima Island, Yamaguchi (34°25'

Table 1
Summary of the proceeding studies on the diets of *Gymnodoris* spp.

Predator	Prey	Condition	Reference
<i>Gymnodoris alba</i> (Bergh, 1877)	<i>Aeolidiella</i> sp.	undescribed	Kay & Young, 1969; Kay, 1979
	<i>Favorinus</i> sp.	undescribed	Kay & Young, 1969; Kay, 1979
	<i>Sakuraeolis modesta</i>	laboratory	Hughes, 1983
	<i>Flabellina alisonae</i>	laboratory	Hughes, 1983
	<i>Phyllodesmium</i> sp.	laboratory	Hughes, 1983
<i>Gymnodoris aurita</i> (Gould, 1852)	<i>Marionia</i> sp.	field	Behrens, 2005
<i>Gymnodoris bicolor</i> (Alder & Hancock, 1866) (< <i>G. citrina</i> ?) ¹	members of <i>Gymnodoris</i>	undescribed	Young, 1969
	<i>Gymnodoris okinawae</i>	undescribed	Young, 1969; Kay & Young, 1969; Kay, 1979
	the egg masses of <i>Gymnodoris okinawae</i>	undescribed	Young, 1969
	<i>Gymnodoris plebeia</i>	undescribed	Young, 1969; Kay & Young, 1969; Kay, 1979
<i>Gymnodoris ceylonica</i> (Kelaart, 1858)	<i>Stylocheilus longicauda</i>	undescribed	Johnson & Boucher, 1983
<i>Gymnodoris citrina</i> (Bergh, 1875)	<i>Gymnodoris citrina</i>	laboratory	Young, 1969
	<i>Gymnodoris citrina</i>	field	Johnson & Boucher, 1983; Johnson, 1992
	<i>Gymnodoris okinawae</i>	field	Johnson, 1992
	<i>Gymnodoris plebeia</i>	field	Johnson, 1992
	several <i>Gymnodoris</i> species	field	Johnson & Boucher, 1983
	unknown <i>Gymnodoris</i> spp.	field	Johnson, 1992
	eggs of other <i>Gymnodoris</i> species	field	Johnson & Boucher, 1983; Johnson, 1992
	eggs of <i>Gymnodoris ceylonica</i>	field	Johnson, 1992
<i>Gymnodoris inornata</i> Bergh, 1880	<i>Chromodoris orientalis</i>	laboratory	Hughes, 1983
	<i>Doriopsilla miniata</i>	laboratory	Hughes, 1983
<i>Gymnodoris okinawae</i> Baba, 1936	various species of the genus <i>Elysia</i>	undescribed	Kay & Young, 1969
	members of Elysiidae	undescribed	Young, 1969
	cephalaspidean	undescribed	Johnson & Boucher, 1983
	did not eat <i>Elysia</i>	laboratory	Johnson & Boucher, 1983
<i>Gymnodoris rubropapulosa</i> (Bergh, 1905)	<i>Hypselodoris iacula</i>	field	Behrens, 2005
<i>Gymnodoris striata</i> (Eliot, 1908)	<i>Plakobranthus ocellatus</i>	field and laboratory	Johnson & Boucher, 1983

¹ *Gymnodoris bicolor* (Alder & Hancock, 1866) is regarded as the junior synonym of *G. citrina* (Bergh, 1875) by many authors (e.g., Risbec, 1953; MacNae, 1958; Baba, 1960), although Young (1969a) described their internal morphologies discriminate *G. bicolor*.

N, 131°13' E), Nagashima Island, Kagoshima (32°13' N, 130°11' E), Kinko-wan Bay, Kagoshima (31°33' N, 130°37' E), Aka-jima Island, Okinawa (26°12' N, 127°17' E), Gahi-jima Island, Okinawa (26°13' N, 127°17' E), and Zamami-jima Island, Okinawa (26°13' N, 127° 17' E). Predators and prey were identified by their external morphology and were photographed *in situ*. Body lengths were measured *in situ* using a ruler or determined from the photographs. We observed the following species: *Gymnodoris ceylonica* (Kelaart, 1858), *G. citrina* (Bergh, 1875), *G. inornata* Bergh, 1880, *G. okinawae* Baba, 1936, *G. rubropapulosa* (Bergh, 1905), *G. striata* (Eliot, 1908; > *G. amakusana* [Baba, 1996]), and an undescribed *Gymnodoris* sp. This undescribed species is often found around the Okinawa Islands and is recognized by its Japanese common name "Shirobonbon-umiushi" (cf. Ono, 2004).

RESULTS AND DISCUSSION

All feeding observations for *Gymnodoris* spp. are summarized in Table 2. We observed sixteen individuals of seven species of *Gymnodoris*. All individuals swallowed the prey whole, even if the prey's body length was the same as that of the predator. In one case of *G. citrina* (No. 3) and in two cases of *G. amakusana* (No. 14 and No. 15), the predators were smaller in body length than their prey and bit off pieces from the prey.

Johnson & Boucher (1983) reported that *G. ceylonica* feeds on the sea hare *Stylocheilus longicauda*; however, we believe they misidentified *S. striatus* (Quoy & Gaimard, 1832) as *S. longicauda*. Because of their similarity in body color, *S. striatus* is often misidentified as *S. longicauda* (Rudman, 1999a), but habitat use

Table 2
Gymnodoris spp. and their preys: field observation.

Predator	No.	Body length	Prey (body length)	Water temperature	Site ¹	Depth ²	Habitat	Date
<i>Gymnodoris ceylonica</i> (Kelaart, 1858)	01	20 mm	<i>Nakanigawata</i> sp. (8 mm)	NR	Aka Is.	6 m	sand	Summer, 2002
<i>Gymnodoris citrina</i> (Bergh, 1875)	02	20 mm	<i>Gymnodoris okinawae</i> (10 mm)	19°C	Hachijo Is.	5 m	rock, occasional coral	6, February, 2002
	03	10 mm	<i>Gymnodoris okinawae</i> (18 mm)	20°C	Hachijo Is.	5 m	rock	April, 2003
<i>Gymnodoris inornata</i> Bergh, 1880	04	12 mm	eggs of nudibranch	NR	Gahi Is.	4 m	dead coral	May, 2001
	05	50 mm	<i>Gymnodoris rubropapulosa</i> (50 mm)	NR	Kinkoh Bay	15 m	rock, occasional sand	Autumn, 2002
<i>Gymnodoris okinawae</i> Baba, 1936	06	50 mm	<i>Dendrodoris fumata</i> (40 mm)	16.8°C	Kinkoh Bay	11 m	mud	8, January, 2006
	07	18 mm	<i>Elysia</i> sp. (18 mm)	20°C	Hachijo Is.	5 m	rock	April, 2003
<i>Gymnodoris rubropapulosa</i> (Bergh, 1905)	08	30 mm	<i>Chromodoris annae</i> (25 mm)	25°C	Hachijo Is.	NR	rock	November, 2004
	09	50 mm	<i>Chromodoris strigata</i> (30 mm)	27°C	Hachijo Is.	10 m	rock	18, June, 2000
	10	30 mm	<i>Chromodoris</i> sp. (20 mm)	25°C	Hachijo Is.	NR	rock	November, 2004
	11	30 mm	<i>Chromodoris</i> sp. (15 mm)	21°C	Hachijo Is.	5 m	rock	30, May, 2006
	12	30 mm	<i>Hypselodoris festiva</i> (15 mm)	25°C	Hachijo Is.	NR	rock	November, 2004
	13	50 mm	<i>Mexichromis multiluberculata</i> (20 mm)	24°C	Gahi Is.	20 m	dead coral	May, 2000
<i>Gymnodoris anakusana</i> ³ (Baba, 1996)	14	20 mm	<i>Elysia ornata</i> (50 mm)	15°C	Ohmi Is.	6 m	muddy sand	21, December, 2003
	15	10 mm	<i>Elysia ornata</i> (40 mm)	12.5°C	Nagashima Is.	10 m	muddy sand, occasional rock	7, January, 2001
<i>Gymnodoris</i> sp.	16	60 mm	<i>Glossodoris cincta</i> (unknown)	22°C	Zamami Is.	15 m	sand	May, 2001

¹ See "materials and method" for details.

² NR, No record.

³ Rudman (1999c) referred *G. anakusana* as a junior synonym of *G. striata*.

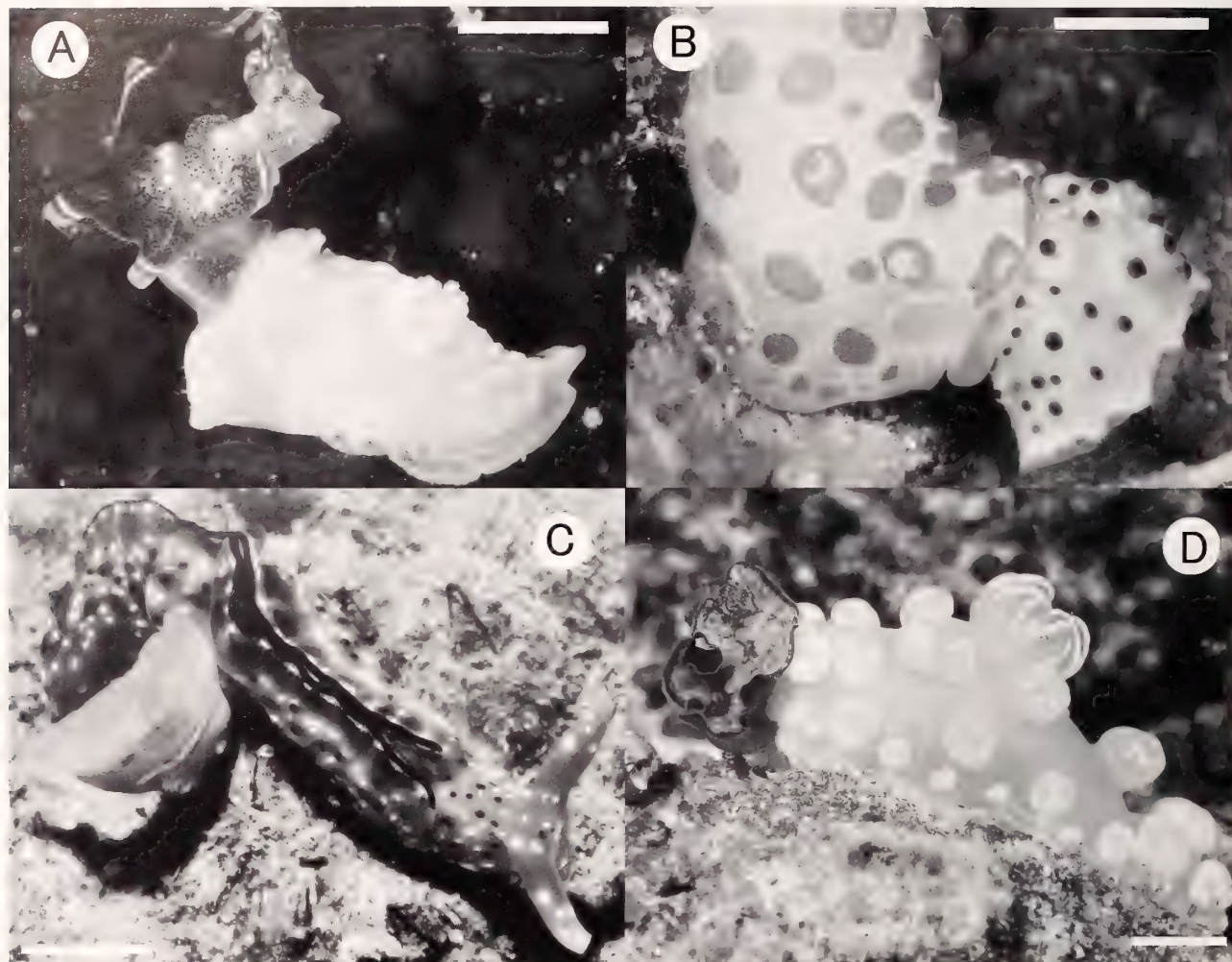


Figure 1. *Gymnodoris* species feeding on opisthobranchs in their natural habitats. (A) *G. okinawae* (right) feeding on a sacoglossan *Thuridilla* sp. (left). (B) *G. rubropapulosa* (left) feeding on *Mexichromis multituberculata* (right). (C) *G. amakusana* (left) feeding on *Elysia ornata* (right). (D) *Gymnodoris* sp. (right) feeding on *Glossodoris cincta* (left). Scale bars = 10 mm.

clearly differs between the species. *Stylocheilus longicauda* is usually found on drifting brown algae in the open ocean, where *G. ceylonica* never occurs (Rudman, 1999b), whereas *S. striatus* is benthic, and is often found with *G. ceylonica*. We observed that *G. ceylonica* feeds on *Nakamigawaia* sp. (Aglajidae, Cephalaspidea). This undescribed species is often found in Japan and is recognized by its Japanese common name "Kurobouzu" (cf. Ono, 1999). *Nakamigawaia* sp. is usually found on the sandy bottom. This observation indicates the possibility that *G. ceylonica* feeds not only on *S. striatus*, but also on other species in the same habitat.

Two individuals of *Gymnodoris citrina* fed on the congener *G. okinawae*, and one individual fed on the eggs of a nudibranch. *Gymnodoris citrina* was reported to feed on several *Gymnodoris* species, including *G.*

okinawae and *G. plebeia*, in the field (Johnson & Boucher, 1983; Johnson, 1992), and on the eggs of congeners, such as *G. ceylonica*, in the field and in aquaria (Young, 1967; Johnson & Boucher, 1983; Johnson, 1992). Moreover, *G. citrina* is cannibalistic. Young (1967) observed a 10-mm specimen consume a 6-mm specimen in an aquarium and reported that this occurrence was probably induced by unnaturally crowded conditions in the aquarium. However, Johnson (1992) observed this behavior in the field, in aquaria, and even in collecting jars, and concluded that cannibalism is normal behavior for *G. citrina*. Thus, it appears that *G. citrina* preys on several congeners and their eggs, as well as on conspecifics.

We observed that *Gymnodoris inornata* fed on *G. rubropapulosa* and *Dendrodoris fumata* in the field. In previous studies, *G. inornata* was reported to feed on

Chromodoris orientalis and *Dendrodoris miniata* (Hughes, 1983), but this was only observed in aquaria. Further field surveys are required to determine whether *G. inornata* feeds on these non-*Gymnodoris* species in nature.

In our field observations, *Gymnodoris okinawae* fed on *Thuridilla* sp. (Sacoglossa; Fig. 1A). This undescribed *Thuridilla* species is commonly found in southern parts of Japan, and is known by its Japanese common name "Fujiro-midorigai" (cf. Ono, 2004). Kay & Young (1969) reported that *G. okinawae* fed on various species of *Elysia* (Sacoglossa). These observations suggest that *G. okinawae* preys on the sacoglossan family Elysiidae. In contrast, Johnson & Boucher (1983) reported that their specimens did not feed on several *Elysia* species in aquaria, but fed on small cephalaspideans in undescribed conditions. We do not know whether their specimens showed normal feeding behavior, because the habitat in which they were observed feeding, i.e., field or laboratory, was not described. Further field studies should be conducted to clarify whether *G. okinawae* feeds on cephalaspideans in nature.

We observed that *Gymnodoris rubropapulosa* fed on *Chromodoris strigata*, *Chromodoris* sp., *Hypselodoris festiva*, and *Mexichromis multituberculata* (Fig. 1B). Behrens (2005) reported that *G. rubropapulosa* fed on *H. iacula*. This species also fed on *Glossodoris rufomarginata*, *H. dollfusi*, *H. krakatoa*, and *M. marieri* (Behrens, personal communication). *Chromodoris* sp. is an undescribed species that is commonly found only in the vicinity of Hachijo-jima Island and the Bonin Islands, and is recognized by its Japanese common name "Kongasuri-umiushi" (cf. Nakano, 2004). These observations suggest that *G. rubropapulosa* feeds on various species of the family Chromodorididae. We observed that *G. amakusana* fed on *Elysia ornata* (Fig. 1C). In contrast, Rudman (1999c) referred to *G. amakusana* as a junior synonym of *G. striata*, which feeds on *Plakobranthus ocellatus* (Johnson & Boucher, 1983). If *G. striata* and *G. amakusana* are synonymous, they may show the same food habits. *Gymnodoris* sp. or Shirobonbon-umiushi differs from all other gymnodorids in shape and color (Rudman, 1999d). It has a white body with many large, puff-like pustules. We observed this species feeding on *Glossodoris cincta*. This is the first observation of its diet (Fig. 1D).

As described above, the diet of each *Gymnodoris* species encompasses a particular range of species. Some *Gymnodoris* species feed on various nudibranchs, whereas others have more selective diets. However, little is known about why and how *Gymnodoris* species identify and select their prey. For instance, Paine (1963) observed that the opisthobranch *Navanax inermis* locates its prey by contact (not distance) chemoreception via the mucus trail of the prey. It is unknown

whether *Gymnodoris* species locate their prey using this same method. To gain a better understanding of the distinct food habits of these opisthobranch opisthobranch-feeders, we should determine how they detect and identify their prey, despite their low mobility.

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Berthella (Opisthobranchia: Pleurobranchidae) from the Northeast Pacific Ocean Prey on Plakinid Sponges (Homoscleromorpha: Plakinidae)

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Abstract. Field observations, laboratory feeding trials, and examination of the gut contents of freshly collected specimens indicate that *Berthella californica* and *B. strongi* from the NE. Pacific Ocean prey on plakinid sponges, including *Oscarella carmela*, a recently described species which lacks skeletal elements. These results strengthen the case that species of *Berthella* are specific to plakinids, especially by documenting the association in a new geographic region. The existence of specific predators of *O. carmela* also supports the hypothesis that this sponge is native to the NE. Pacific Ocean but was previously overlooked or misidentified in the wild.

INTRODUCTION

Pleurobranch opisthobranchs in the genus *Berthella* are widespread, often conspicuous members of the benthic epifauna (Thompson, 1976; Willan, 1984). The prey of only four species has been determined with certainty (Delaloi & Tardy, 1977; Willan, 1984; Cattaneo-Vietti, 1986; Picton, 2002; Goddard, 2005). These records, which come from the Mediterranean Sea, NE. Atlantic, and SW. Pacific Ocean, suggest that species of *Berthella* prey specifically on plakinid homoscleromorph sponges, which according to recent studies are genetically more similar to the Eumetazoa than to the rest of the Porifera (Nichols et al., 2006; Sperling & Peterson, in press). A few species of *Berthella* have also been surmised to feed on ascidians, based on (1) the known diets of species of the related *Pleurobranchus* (Thompson, 1976; Thompson & Colman, 1984), and (2) reports of association with ascidians in the field (MacFarland, 1966; Behrens & Hermosillo, 2005). However, actual consumption of ascidians by species of *Berthella* has not been observed, and the simple occurrence of grazing opisthobranchs on sessile organisms is insufficient to infer direct predation, especially in space-limited, encrusting communities where overgrowth of one species by another is common (e.g., Rützler, 1970; Jackson, 1977; Russ, 1982).

Nothing has been published previously on the diets of *Berthella* from the northeast Pacific Ocean. Here I present field and laboratory observations on the diets of *Berthella californica* (Dall, 1900) and *B. strongi* (MacFarland, 1966). *Berthella californica* is a conspicuously colored species that reaches 50 mm in extended length and ranges from the Sea of Japan, across the north Pacific, and into the eastern Pacific as far south as the Galapagos archipelago (Martynov, 1998; Behrens & Hermosillo, 2005; Camacho-Garcia et al., 2005). *Berthella strongi* is drab in color compared to *B.*

californica, reaches 25 mm in extended length, and ranges from Vancouver Island, British Columbia to Punta Rosarito on the Pacific coast of Baja California (Behrens & Hermosillo, 2005).

METHODS AND RESULTS

1. *Berthella californica*

Field observations and observations of gut contents: While studying the intertidal opisthobranchs of Cape Arago, Oregon (43°20'N, 124°22'W), I found numerous specimens of *Berthella californica* (Goddard, 1984; unpublished observations), but recorded only two individuals associated with potential prey items. One of these was found in July 1998 on the thinly encrusting compound ascidian *Diplosoma listerianum*; the other in August 1986 under a cobble next to a thin, tan-colored slimy sponge. This sponge has recently been described from Monterey Bay, California by Muricy & Pearse (2004) as *Oscarella carmela*. However, no evidence of feeding on either of these organisms was observed on these dates.

I also examined microscopically the fecal strands of three specimens freshly collected from Cape Arago in April 1991 (using 6% NaOCl to clean any skeletal elements and acetic acid to differentiate calcareous from siliceous spicules). From one individual these contained a mixture of poeciloscleridan sponge spicules, including an unidentified hymedesmiid, and a few spicules characteristic of the thinly encrusting *Zygherpe hyaloderma*. From another, they contained some siliceous diod spicules characteristic of a plakinid homoscleromorph sponge (Austin & Ott, 1987; Muricy et al., 1998) and from the third, numerous siliceous triods characteristic of a plakinid (Austin & Ott, 1987; Muricy et al., 1998), as well as a few spicules from unidentified poeciloscleridan sponges. Additionally, I

dissected the alimentary tract of one specimen freshly collected in February 1987 from an unidentified sponge at Cape Arago by T.A. and K.R. Wayne and found no recognizable contents other than a few sand grains.

Laboratory feeding trials: To test whether or not *Berthella californica* prey on *Oscarella carmela*, I collected from the protected rocky shore at Cape Arago one specimen of the sponge on 25 June 2006 and two specimens of the slug on 27 June 2006 and conducted a simple feeding experiment at the Oregon Institute of Marine Biology. At 12 noon on 27 June, I placed one 22 mm long specimen of *B. californica* with a 1 cm² piece of *O. carmela* in a shaded 8 × 8 × 14 cm high, plastic container (with mesh covered openings to allow water exchange) on an indoor, black, flow-through water table at ambient ocean temperature (approximately 12°C). Within 1 hr the slug had found and consumed most of the sponge, and after another 1.5 hr had consumed the remainder. This slug was preserved 1.25 hr after finishing the sponge and later deposited in the California Academy of Sciences (CASIZ 173046). Starting at 4:30 pm the same day, I repeated this with the second slug, also 22 mm long. This specimen did not feed on (or even appear to locate) *O. carmela* over the next 22 hr. I then placed the two in direct physical contact, and the slug immediately positioned its oral veil over the sponge and began to feed. After 5 min I removed the sponge and replaced it with a similarly sized piece of *Halisarca sacra*, a thin, tan-colored dendroceratid slime sponge superficially similar to *O. carmela* in its color, thinness and lack of skeletal elements. After 15 min the slug had not attempted to feed on this sponge. I then replaced the *Halisarca* with the *O. carmela*, and the slug immediately began feeding again. Two and a half hr later, the slug had consumed the entire piece of *O. carmela*. I then placed a piece of *Halisarca* with the slug. After two days with no sign of feeding, I placed the anterior end of the slug in contact with the *Halisarca*. The slug slowly but steadily turned away from the sponge and crawled away. I left the *Halisarca* and the slug in the same container for an additional 6 days, during which there was no evidence of feeding on the sponge.

For comparison to the above trials, I placed in an identical container for the same 10-day time period three specimens of the dorid nudibranch *Hallaxa chani* with one piece each of *Halisarca sacra* and *Oscarella carmela*. *Hallaxa chani* specializes on *Halisarca sacra* (Goddard, 1981, 1984, 1998; as *Halisarca* sp.). These slugs quickly consumed all of the *Halisarca*, but did not eat any *O. carmela* during the 10-day period. I then preserved the *Hallaxa chani*, the *O. carmela*, and an additional piece of *Halisarca sacra* from Cape Arago and deposited them in the California Academy of Sciences (CASIZ 173047, 173045, 173043, respectively).

2. *Berthella strongi*

On 7 October 2006 I found one specimen of *Berthella strongi*, 5 mm long, on *Oscarella carmela* on the underside of a low intertidal cobble in a boulder field located 2 km west of the Ellwood Pier (34°25.80'N, 119°55.36'W), Goleta, Santa Barbara County, California. I collected the sponge with the slug and held them together in a shaded dish of seawater at 18°C for one day. During this time the slug moved only slightly from its original position and, as observed under a dissecting microscope, had grazed overnight a small portion of the sponge. The slug and the sponge were then preserved and deposited together in the Santa Barbara Museum of Natural History (SBMNH 369472).

On 4 November 2006 I found three additional specimens of *Berthella strongi*, 6, 10 and 10 mm long, all in contact with *Oscarella carmela* underneath three different rocks in the low intertidal at the Ellwood boulder field. I collected all three specimens and held them separately with 67, 67 and 75 mm² of *O. carmela*, respectively, in glass finger bowls of seawater at 16–19°C for 2.5 days. Approximately 75 mm² of *O. carmela* was held separately in another finger bowl as a control. The sponges were found adjacent to the slugs, attached to fragments of rigid, sand-encrusted, polychaete worm tubes. The finger bowls were covered by a damp cloth, shaded, and their water changed daily. The position of the slugs (on or off *O. carmela*) was checked 4 times daily. The 6 mm slug and one 10 mm slug spent the entire 2.5 days on *O. carmela*, consuming 17 and 60 mm² of the sponge, respectively. The other 10 mm specimen spent all but a few hours of day two on the sponge and also consumed 60 mm². The control sponge showed no change in area during the experiment. At the conclusion of the feeding experiment, the 6 mm slug and the remainder of its sponge prey were preserved in 70% ethanol and deposited together in the Santa Barbara Museum of Natural History (SBMNH 369473), as was the *O. carmela* used as a control (SBMNH 369474).

DISCUSSION AND CONCLUSIONS

All four *Berthella strongi* found in this study were associated with *Oscarella carmela* in the wild and readily consumed this sponge in the laboratory. *Berthella californica* also consumed *Oscarella carmela* in the laboratory, and given one record of its occurrence next to this sponge at Cape Arago, likely also preys on *O. carmela* in the wild. Additionally, A. Draeger recently found a mating pair of *B. californica* next to *O. carmela* at 9 m depth in Monterey, California (J. S. Pearse, personal communication, 29 June 2006). *Oscarella carmela* lacks skeletal elements and would therefore be missed in examination of gut contents, possibly explaining the lack of recognizable

gut contents in the specimen of *B. californica* collected from an unidentified sponge at Cape Arago in February 1987.

Evidence in the field of feeding by *Berthella californica* was sparse compared to that for other Nudipleura (Wägele & Willan, 2000) at Cape Arago (personal observations). However, *O. carmela* is thin, drab in color, and easily overlooked without an established search image, especially when grazed (Muricy & Pearse, 2004; personal observations). Moreover, observations were made primarily during the day, and many species of *Berthella* and other pleurobranchs are nocturnal, taking refuge under rocks during the day (Delaloi & Tardy, 1977; Willan, 1984; R. Willan, personal communication). Additionally, *O. carmela* appears to be rare at Cape Arago (personal observations), and except for the skeletal evidence of plakinids in the fecal strands of *B. californica*, other species of plakinid sponges have not been observed at this locality. *Berthella californica* may be effectively limiting the abundance of plakinids intertidally at Cape Arago, and the most *B. californica* observed there at any one time were (on two occasions) crawling out in the open, in boulder field sea urchin barrens before sunrise (personal observations).

The feeding trials conducted in this study commenced the same day the slugs were collected. Consequently, the difference in the initial responses of the two specimens of *B. californica* to the presence of *O. carmela* may simply have reflected the time period since each had last fed in the field. However, dissimilar diets in the wild and ingestive conditioning (Hall et al., 1982) might also explain this difference. The gut contents observed in this study indicate that at least some individuals of *B. californica* ingest other plakinid sponges, species of which have been recorded previously from the northeast Pacific Ocean (Austin & Ott, 1987; Lehnert et al., 2005).

Given the nocturnal habits of many pleurobranchs (Willan, 1984), the midday feeding activity by *B. californica* at the outset of the first feeding trial may have been atypical, even for a potentially very hungry slug. However, both feeding trials were conducted in shaded containers held on a black seawater table, and only diffuse, indirect light was used for observation.

Overall, the results reported here strengthen the case that species of *Berthella* are specific to plakinids, especially by documenting the association in a new geographic region. The presence of poecilosclerid sponge spicules in the fecal strands of some individuals of *B. californica* seem likely to have resulted from the incidental ingestion of these sponges, particularly where they may have been overgrown or were otherwise in close contact with a plakinid. However, additional observations and feeding trials are needed to more fully document the diet of both *B. californica* and *B. strongi*.

Given MacFarland's (1966, p. 91) observation that *B. strongi* occurs "upon or near compound ascidians," as well as the single record noted above of *B. californica* on *Diplosoma listerianum*, feeding trials might also include compound ascidians. However, it should be noted that *Oscarella carmela*, whose type locality on the Monterey peninsula lies within a few km of where MacFarland collected *B. strongi*, has a slippery, gelatinous texture and has sometimes been mistaken for thinly encrusting compound ascidians (Muricy & Pearse, 2004, p. 609; S. Anderson, personal communication 2 November 2006). Moreover, compound ascidians are often more conspicuous in the under-rock habitat favored by these *Berthella* species than the thin, tan-colored *O. carmela* (personal observations). Finally, as mentioned previously, no *Berthella* species have ever been observed to actually consume ascidians, and for grazing predators of sessile epifauna, substratum often does not equate with prey.

Oscarella carmela was first observed in California in the 1980s in the seawater systems at the Long Marine Laboratory and Monterey Bay Aquarium, leading to questions as to whether the sponge is native or introduced to the NE. Pacific Ocean (Muricy & Pearse, 2004). Predation by *B. californica* and *B. strongi* on *O. carmela*, combined with additional locality records of the sponge from outer coast sites throughout California (personal observations), support the hypothesis that the sponge is native to this region, but had previously been overlooked or misidentified as either a compound ascidian or the dendroceratid slime sponge *Halisarca*.

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Effects of Increased Salinity on Survival and Lipid Composition of *Helisoma trivolvis* (Colorado Strain) and *Biomphalaria glabrata* in Laboratory Cultures

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Abstract. High performance thin layer chromatography (HPTLC) was used to study the effects of increased salinity on the lipid composition of the digestive gland-gonad complex (DGG) of *Biomphalaria glabrata* (NMRI strain) and *Helisoma trivolvis* (Colorado strain) snails. Both species of snails were maintained in laboratory cultures containing various dilutions of artificial ocean water (AOW) for up to 2 weeks. Controls consisted of snails maintained identically in deionized water (DI). Both species of snails maintained in AOW at a salinity of 20‰ (196 mOsmol/kg) showed no significant changes in the concentrations of the major neutral lipid and phospholipid classes compared to snails maintained in DI. Apparently, the ability to survive for 2 weeks at 20‰ salinity had no noticeable effect on the concentrations of the depot or structural lipids associated with the DGG of these snails. Snails of both species were dead at 100, 50 and 25‰ salinities within 90 min. At a salinity of 20‰, 3 of 8 *B. glabrata* and 4 of 8 *H. trivolvis* survived for 2 weeks; at 10‰ salinity, 6 of 8 *B. glabrata* and 7 of 8 *H. trivolvis* survived for 2 weeks. Most snails of both species survived for 2 weeks in DI. The ability of planorbid snails to survive relatively high salinities has implications for the spread of larval trematodiasis to endemic areas where salinities may be elevated.

INTRODUCTION

Increased salinity in fresh water lakes and ponds is recognized as a serious environmental problem worldwide (Williams, 1987). The question of how large an increase in salinity can be tolerated by most fresh water snails has not been well explored. In our laboratory, we use two species of fresh water snails for various biological and chemical studies. These snails are an NMRI strain of the medically important planorbid *Biomphalaria glabrata* (Say, 1816) and a Colorado strain of the economically important planorbid *Helisoma trivolvis* (Say, 1816). Schneck & Fried (2005) recently described the growth of both of these snail species under the same laboratory conditions.

Our laboratory has examined the effects of various parameters on the lipid content of *B. glabrata* and *H. trivolvis*, i.e., larval trematode parasitism, different diets, snail age, starvation, and estivation. As reviewed in Bandstra et al. (2006a), alterations in lipids, i.e., increase or decrease in the concentrations of particular lipid classes, occur as a function of some of the aforementioned parameters. With this in mind, one purpose of our study was to determine the effects of increased salinity on the lipid content of *B. glabrata* and *H. trivolvis*. Because information on the tolerance of planorbid snails to increased salinities is relatively

sparse, another purpose of this study was to examine the effects of increased salinity on the survival of *B. glabrata* and *H. trivolvis* in the laboratory.

MATERIALS AND METHODS

Stock cultures of *B. glabrata* (NMRI strain) and *H. trivolvis* (Colorado strain) were maintained in the laboratory as described in Schneck & Fried (2005). Adult snails (11 ± 1 mm in shell diameter) of both species were maintained, 4 or 5 snails per culture, in 8.5 cm diameter finger bowls each containing 100 ml of different concentrations of artificial ocean water (AOW) at $22 \pm 1^\circ\text{C}$. The AOW was purchased as a prepared concentrate of artificial salts (Instant Ocean) from Aquarium Systems (Mentor, OH). A stock solution of AOW was made using 43.13 g of Instant Ocean in 1 L of deionized (DI) water to represent full strength sea water with an osmolality of 960 mOsmol/kg. The full strength sea water was diluted using DI water to obtain dilutions of 50, 25, 20, 15, 10, and 5‰ sea water with osmolalities of 499, 251, 196, 151, 100, and 40 mOsmol/kg, respectively. The osmolalities of the AOW solutions were measured using a Wescor Inc. (Logan, UT) vapor pressure osmometer. For both the survival and lipid-high performance thin layer chromatography (HPTLC) studies, a group of 4 snails of each species was maintained in separate cultures at most salinities for up to 2 weeks. Survival

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data determined the salinity that was used in the HPTLC-lipid studies. Cultures were fed romaine lettuce leaves ad libitum and the water was changed every two days. Snails were examined daily for 1 to 14 days after the cultures were set up. Dead snails were removed from the culture on the same day they died. Snails that did not react to mechanical probing were considered dead. Controls for the salinity studies consisted of snails maintained identically but in DI.

For HPTLC analysis, snail digestive gland-gonad complexes (DGGs) were obtained and used as described in Ong et al. (2006). Three DGGs of each snail species ($n = 3$) maintained in 20% AOW and DI water were prepared for the neutral lipid analysis, and three snail DGGs of each species ($n = 3$) for analysis of the phospholipids. The use of the 20% AOW was based on the relatively good survival of both snail species for 2 weeks at this salinity (see Results for further information). The blotted wet weight of the *H. trivolvis* snails ranged from 9.8–19.7 mg and the *B. glabrata* ranged from 8.0–23.9 mg. Each sample consisted of a single DGG and was prepared in a tissue grinder (15 mL, KT885300-0015, VWR International, Inc., West Chester, PA, USA) using chloroform-methanol (2:1) with a volume that was twenty times the weight of the sample. After homogenization, the supernatant was filtered through cotton, and a volume of Folch wash (0.88% KCl) was added that was $\frac{1}{4}$ that of chloroform-methanol (2:1) used for lipid extraction. The upper hydrophilic layer was removed using a Pasteur pipet and discarded; the lower lipophilic layer was dried under nitrogen gas in a water bath (40–60°C). Residues were reconstituted with 80–200 μL of chloroform-methanol (2:1), the exact volume chosen based upon the amount of the residue.

For neutral lipid analysis, the standard was Non-Polar Lipid Mixture-B (Materya Inc., Pleasant Gap, PA, USA), which contained 20.0% each of cholesterol (CH), oleic acid (OA), triolein (TO), methyl oleate (MO), and cholesteryl oleate (CO) with a total lipid concentration of 25.0 mg/mL. These compounds were used to represent free sterols, free fatty acids, triacylglycerols, methyl esters, and steryl esters, respectively. The standard was dissolved in a 25.0 mL volumetric flask in chloroform-methanol (2:1) to yield a final concentration of 0.200 $\mu\text{g}/\mu\text{L}$ of each compound.

Analysis was performed on HPTLC silica gel 60 CF_{254} channeled silica gel plates (EMD Chemicals, Inc., Gibbstown, NJ, an affiliate of MerckKGaA, Darmstadt, Germany), 10 \times 20 cm, with a preadsorbent zone and 19 scored lanes. Plates were prewashed by development to the top with methanol and dried in a fume hood. Standards of neutral lipids were applied with a 10.0 μL Drummond (Broomall, PA, USA) digital microdispenser onto the preadsorbent of sepa-

rate lanes in aliquots of 1.00, 2.00, 4.00, 8.00, and 16.0 μL , and reconstituted samples were applied in 2.00 μL –16.0 μL aliquots. Applied aliquots were allowed to dry for 30 s before development of the plate in a rectangular Camag (Wilmington, NC, USA) HPTLC twin-trough chamber that was lined with a saturation pad (Analtech, Newark, DE, USA) and allowed to equilibrate with the mobile phase for at least 15 min before inserting the plate. The mobile phase, petroleum ether-diethyl ether-glacial acetic acid (80:20:1), was allowed to reach a level 9 cm above the preadsorbent-silica gel interface, which required approximately 10 min. Developed plates were dried in a fume hood for 1 min using cool air from a hairdryer and sprayed with 5% ethanolic phosphomolybdic acid (PMA) solution. The plate was heated for at 115°C on a Camag plate heater until blue neutral lipid bands appeared on a yellow background.

The standard for polar lipid analysis, Polar Lipid Mix (Materya, Inc., Pleasant Gap, PA, USA), contained 25.0% each of CH, phosphatidylethanolamine (PE), phosphatidylcholine (PC), and lysophosphatidylcholine (LPC) with a total of 25.0 mg of lipid. The standard was placed in a 25 mL volumetric flask and diluted with chloroform-methanol (2:1) to prepare a solution containing 0.0250 $\mu\text{g}/\mu\text{L}$ of each lipid. HPTLC analysis of polar lipids was done on the same plates and with the same standard and sample volumes as described previously for the neutral lipids, but the mobile phase was chloroform-methanol-water (65:25:4) with a development time of approximately 20 min. The dried plates were sprayed with a 10% cupric sulfate solution and then heated at 140°C until brown bands on a white background were formed.

To quantify the amount of lipid in samples, a Camag TLC Scanner II was used with the following settings: tungsten light source at 610 nm for neutral lipids and deuterium light source at 370 nm for polar lipids, slit width 4, slit length 4, and scanning speed 4 mm/sec. The CATS-3 software was used to generate a linear regression calibration plot by relating the weights of the standard zones to their peak areas. From the calibration plot, the weights of the sample zones were automatically interpolated based on their measured peak areas. After the data was collected, if more than one aliquot of a single sample fell within the calibration curve, the weight corresponding to the sample area closest to the mean of the two middle standard areas was used for the calculation of lipid percent. The weight percentages of neutral and polar lipids in the whole snail DGGs were calculated using the following equation:

$$\% \text{ Lipid} = \frac{(w)(R)(F)(100)}{\mu\text{g sample}}$$

Table 1

Weight percent (mean \pm SE) of neutral and polar lipids in the DGGs of *B. glabrata* (Bg) and *H. trivolvis* (Ht) in 20% artificial ocean water (AOW) and deionized water (DI).

Snail	FS	TG	PC	PE
Ht in AOW	0.0766 \pm 0.0243	0.239 \pm 0.0407	0.6846 \pm 0.135	0.201 \pm 0.0343
Ht in DI	0.0742 \pm 0.00504	0.153 \pm 0.101	0.5973 \pm 0.059	0.352 \pm 0.099
Bg in AOW	0.0753 \pm 0.0048	0.1697 \pm 0.0621	0.8023 \pm 0.311	0.4235 \pm 0.0172
Bg in DI	0.0679 \pm 0.0172	0.2214 \pm 0.0776	1.288 \pm 0.139	0.32234 \pm 0.153

FS = Free sterols.

TG = Triacylglycerols.

PC = phosphatidylcholine.

PE = phosphatidylethanolamine.

n = 3 samples for each analysis.

where $w = \mu\text{g}$ interpolated from the plot and $R = [\text{reconstituted volume } (\mu\text{L})]/[\text{spotted volume } (\mu\text{L})]$. For quantification of some samples, dilution or concentration was necessary in order to have scan area of at least one sample aliquot bracketed within the calibration plot. In these cases, a suitable factor (F) was included in the calculations.

RESULTS

Survival data was as follow: all snails ($n = 4$ for each species at each salinity) were dead at salinities of 100, 50, and 25% S within 90 min. A marked difference occurred at 20% salinity where 3 of 8 *B. glabrata* (37.5%) and 4 of 8 *H. trivolvis* (50%) survived the 2 week experimental period. Because of the relatively high survival in 20% salinity, it was this salt concentration that was selected for the lipid-HPTLC studies. Additional survival data showed that at 10% salinity, 6 of 8 (75%) *B. glabrata* and 7 of 8 (87.5%) *H. trivolvis* survived for 2 weeks. Controls in deionized water showed the following survival data at 2 weeks: 8 of 8 *B. glabrata* (100%) and 7 of 8 *H. trivolvis* (87.5%).

In the HPTLC studies, the major lipids quantified were free sterols (FSs), (TGs), PC and PE. The linear regression calibration plots relating the scan areas to weights of neutral lipid standard zones (0.400–3.20 μg) and polar lipids (0.500–4.00 μg) consistently gave linear regression correlation (r) values of 0.98 and 0.99, respectively.

Samples analyzed for neutral lipids showed zones that comigrated with standards with R_f values of 0.19 (CH) and 0.57 (TO) in every sample. Some samples had low amounts of free fatty acids that comigrated with the oleic acid standard at R_f 0.38. The faster moving neutral lipid sample zones, tentatively thought to be steryl esters and methyl esters, did not comigrate with CO and MO, respectively in the neutral lipid solvent system. These zones were relatively sparse in the snail

samples, and since their identities were uncertain, they were not further characterized.

Samples analyzed for polar lipids showed zones with comparable migration to the standard with R_f values of 0.28 (PC) and 0.47 (PE). LPC was not able to be detected with the cupric sulfate reagent at the concentrations applied.

Table 1 shows the lipid percent \pm standard error data of FS, TG, PC, and PE fractions of the DGGs of *H. trivolvis* and *B. glabrata* DGGs of snails maintained in 20% saline and DI water. The greatest concentrations in both species of snails were the phospholipids.

In spite of apparent differences in the means of certain values of some lipids in snails maintained in 20% saline versus DI water (for instance triacylglycerols from *H. trivolvis* snails, PC from *B. glabrata* snails and PE from *H. trivolvis* snails), Student's t -test ($P > 0.05$) showed no intraspecific differences in the concentration of any lipids in snails maintained in the 20% saline solution versus those in DI water for the 2 week period.

DISCUSSION

Relatively few studies are available on the survival of fresh water pulmonates at various salinities. Of the pulmonate snails previously studied, *Lymnaea peregra* (Müller, 1774) was able to survive up to 10–11 parts per thousand (ppt) and *Physa fontinalis* (Linnaeus, 1758) survived up to 6 ppt (Hyman, 1967). Our study showed good survival of *H. trivolvis* and *B. glabrata* at 10 ppt and moderate survival of both species at 20 ppt. A marked reduction in survival was seen in both species at 25 ppt, compared to 20 ppt. We can offer no explanation at this time for such a dramatic difference in survival at 25 versus 20 ppt salinities.

The results of our HPTLC-lipid studies showed no significant changes in the concentrations of phospholipids and neutral lipid classes in the DGGs of *B. glabrata* and *H. trivolvis* maintained in DI versus 20%

saline. Our results on the effects of salinity on the lipid class composition in the DGGs of planorbids contrast noticeably to other studies, i.e., snail aging (Schneck et al., 2004), larval trematode parasitism (Bandstra et al., 2006b), and estivation and starvation (White et al., 2006), which showed significant increases or decreases in the concentration of one or more lipid classes in *B. glabrata* and *H. trivolvis* snails as a function of the variable studied (see Bandstra et al., 2006a for a review). We conclude that adaptation of these snails to the different salinities used in our study did not interfere with the biochemistry of the lipid depot storage involving neutral lipids or the integrity of the structural lipids involving phospholipids.

Survival of *B. glabrata* in our study at 10 and even 20 ppt is of interest because de (da Silva et al., 2006) showed survival of this medically important snail from aquatic environments in coastal areas of Brazil at a salinity of 7.7 ppt. These authors were concerned that survival of *B. glabrata*, the vector of *Schistosoma masoni*, at such a relatively high salinity constitutes an increased risk for the spread of schistosomiasis in endemic waters where salinity may be elevated.

Although we did not monitor food intake or fecundity of our snails, we made incidental observations on feeding and egg laying under saline versus DI water conditions for both species of snails. Quantitatively, we found no differences in food intake or numbers of egg masses in our snail cultures maintained under saline versus DI conditions. Such findings indicate that these snails showed a reasonable tolerance to such relatively high salinities, at least under laboratory conditions. We were also surprised at how well both species of snails survived under experimental conditions for 2 weeks in DI. We have always used ASW as described by Ulmer (1970) to culture our planorbids (see Schneck & Fried, 2005 for a review). Perhaps for short term maintenance of *H. trivolvis* and *B. glabrata*, the simpler medium of DI may be useful for snail maintenance as is the more complex ASW.

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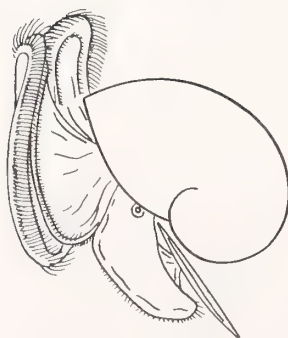
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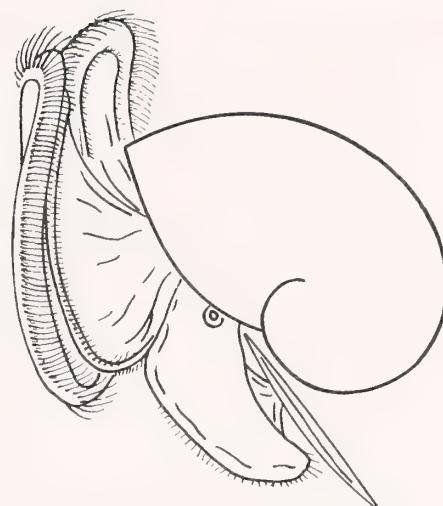
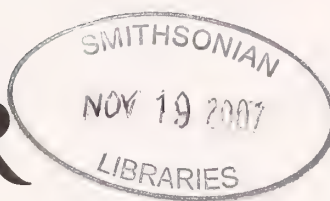


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The Genus *Paradoris* Bergh, 1884 (Nudibranchia: Discodorididae) in the Tropical Americas, and South Africa with the Description of a New Species

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Abstract. A new species of *Paradoris* Bergh, 1884, *P. caeruleus* sp. nov. is described based on specimens collected from South Africa. The coloration, radular morphology, and details of the reproductive system of this species differ significantly from other previously described *Paradoris* species by having a blue body with gray-blue spots and a few black spots on the dorsum, as well as an accessory gland with two stylets in each sac. A redescription of *P. mulciber* and *P. lopezi* is based on newly collected material of these species from the Caribbean coast of Costa Rica and the Galápagos Islands. The range of *P. lopezi* is extended, from Mexico to the Galápagos Islands.

INTRODUCTION

A taxonomic revision of *Paradoris* Bergh, 1884, recently published by Dayrat (2006) recognizes eight species from the Pacific, Atlantic, and Indo-Pacific oceans: *P. indecora* (Bergh, 1881); *P. dubia* (Bergh, 1904); *P. liturata*, (Bergh, 1905); *P. erythraeensis* (Vayssi re, 1912); *P. mulciber* (Marcus, 1970); *P. tsurugensis* Baba, 1986; *P. araneosa* Vald s, 2001; and *P. lopezi* Hermosillo & Vald s, 2004. According to Dayrat (2006), *Paradoris* is characterized by the following combination of characters: labial armature with three jaw plates, radula elongated and narrow, grooved outer edge of the hook of the lateral teeth, and grooved oral tentacles.

The first reference to *Paradoris* in the Western Atlantic Ocean was the description of *Paradoris mulciber* from Brazil (Marcus, 1970), originally described as the type species of the new genus *Percunas* Marcus, 1970. Later, Marcus (1976) synonymized *Percunas* with *Paradoris*. Ortea (1995) revised the species of the genus from the Canary Islands. According to this author, there were four species in this area, however Dayrat (2006) synonymized three of these species with *P. indecora*, based on individual variation. This author, as well as Ortea (1995), also concluded that *Paradoris granulata* Bergh, 1884, the type species of the genus, is a junior synonym of *Discodoris indecora* Bergh, 1881.

The first reference of this genus in the Pacific Ocean was the description of *Paradoris tsurugensis* from Japan by Baba (1986, 1989). Later, Miller (1995) described *Paradoris leuca* from New Zealand, which was

synonymized most recently with *Paradoris dubia* (Bergh, 1904) by Dayrat (2006) based on similarities of the reproductive system. Vald s (2001) described two new species from deep waters of New Caledonia: *Paradoris araneosa* and *Paradoris imperfecta*; the latter was synonymized with the former by Dayrat (2006). Finally, Hermosillo & Vald s (2004) described *Paradoris lopezi*, a new species from Mexico.

Paradoris mulciber (Marcus, 1970) is known only from the type material described from Brazil and redescribed by Dayrat (2006). This species and *Paradoris lopezi* Hermosillo & Vald s, 2004 are the only two members of the genus *Paradoris* reported from the Americas. The present paper redescribes these species on the basis of several new specimens collected from the Caribbean coast of Costa Rica and the Gal pagos Islands, Ecuador, respectively. We also describe one new species from South Africa.

MATERIALS AND METHODS

The material studied is deposited at the Zoology Museum of the University of Costa Rica, the Department of Invertebrate Zoology and Geology of the California Academy of Sciences, San Francisco, USA (CASIZ), and the Natural History Museum of Los Angeles County (LACM).

Specimens were preserved in 70% ethanol. They were dissected by dorsal incision, and their reproductive systems were examined and drawn under a dissecting microscope with camera lucida. At least two specimens of each species were examined anatomically and dissected for this study. The buccal masses were

dissected and immersed in sodium hydroxide, rinsed, and then mounted on stubs for SEM examination.

The accessory gland from the reproductive system was dissected and placed in different concentrations of alcohol for at least 20 min and then transferred to a solution of xylol for 20 min. After the tissue became translucent, the gland was mounted on a cover slide. The stylets were drawn using a microscope with camera lucida.

SPECIES DESCRIPTIONS

Genus *Paradoris* Bergh, 1884

Paradoris multiciber (Marcus, 1970)

(Figures 1A, 2, 3, 4)

Type material examined: *Holotype*: Juriaçu, Maranhão Province, Brazil 00°04'S, 44°33'W, 6 September 1967, 1 specimen (previously dissected), 21 mm preserved length, *leg.* Almirante Saldanha R/V (MZSP 41291).

Other material examined: Ponta de Pedra, PERNAMBUCO Province, Brazil, 30 August 1970, 1 specimen (previously dissected), 35 mm preserved length, *leg.* Montonchet (MZSP 41292, # 1045 Marcus Coll.); Manzanillo, Área de Conservación Amistad Caribe, Sixaola, Limón, Costa Rica (9°38'42"N, 82°39'29"W), 20 October 1998, 4 specimens (3 dissected), 27–56 mm preserved length, collected under rocks by SCUBA, 9 m depth, *leg.* S. Avila (INB001501499); Silal de Cahuita, Parque Nacional Cahuita, Limón, Costa Rica (9°44'35"N, 82°48'21"W), 21 September 1999, 2 specimens (one dissected) 15–29 mm preserved length, collected under rocks by SCUBA diving, 12.5 m depth, *leg.* M. Calderón (INB001496697).

Geographic range: This species was previously known from Brazil (Marcus, 1970, 1976) and Costa Rica (Espinosa & Ortea, 2001). Some additional specimens have been collected from the Caribbean (Vinicius Padula, personal communication).

External morphology: Living animals range from 20–60 mm long. The body is oval and elevated, widest in the middle region (Figures 1A, 2A). The mantle margin is wide, undulating, and spiculose. The dorsum is covered with rounded, widely spaced tubercles of various sizes. The largest ones are generally situated in the middle region of the notum (Figure 2A), and most of them are elevated. Some specimens have one or two tubercles located anteriorly and posteriorly on the rhinophoral sheath. The rhinophores have 19–21 very thin lamellae. The rhinophoral and branchial sheaths are undulate. The gill consists of six tripinnate branchial leaves. Other specimens examined have around the same number of lamellae in the rhinophores

and branchial leaves. The oral tentacles are finger-like and have a longitudinal groove on their external side. The anterior border of the foot is grooved and notched (Figure 2B). The foot is completely covered by the notum when the animal is in motion.

The background color of the dorsum in living animals is light brown to pale cream, with numerous small dark brown spots (Figure 1A) very densely arranged on the entire dorsum and at the base of the tubercles. Each spot itself is composed of an aggregation of minute brown specks. The apices of large tubercles are yellowish. The rhinophores and branchial leaves are pale brown with small, dark brown spots arranged irregularly. The tips of the branchial leaves are yellowish, and the branchial sheath is undulate. The ventral side of the animal is cream colored. The sole of the foot has more dark spots than the hyponotum, but they are smaller (Figure 2B). The same spotting occurs on the ventral surface, foot, and mantle. The tentacles are covered with brown speckles.

Anatomy: The jaw has three distinct pieces with a number of simple, regularly arranged elements about 8 μ m in length (Figure 3A). The radular formula of an 18 mm preserved length specimen is $55 \times (18.0.18)$ (INB001501499) and a 40 mm preserved length specimen is $47 \times (16.0.16)$ (LACM ACC 4308). In general, the teeth are broad and hook-shaped. All the lateral teeth, including the outermost, are smooth. They become gradually larger from the innermost to the mid-laterals, then become smaller and less angular from the mid-laterals to the outermost. The innermost teeth are thin, pointed, and angular (Figure 3B). The mid-lateral teeth have a groove on the lower side of the cusp (Figure 3C). The outermost have a prolongation on the upper side of the teeth (Figure 3D). There is no sharp distinction between the base and the cusp in the outermost tooth.

The ampulla, which is long and tubular, is located left on top and anterior to the female glands and next to the bursa copulatrix. The deferent duct is large and thin throughout its length (Figure 4A) and leads to a granular and convoluted prostate that is folded upon itself. At the distal end, there is an unarmed penis that is wider than the rest of the duct. The long vagina connects to two accessory glands and three muscular sacs containing one stylet each (Figure 4B). Two of the sacs are located on the dorsal side and one on the ventral side of the vagina. Each stylet is about 0.6 mm in length. The whitish bursa copulatrix is semi-spherical and thin-walled. From the bursa copulatrix leads another thin duct that connects to the oval seminal receptacle and the uterine duct.

Remarks: *Paradoris multiciber* (Marcus, 1970) is the only species of the genus *Paradoris* reported from the

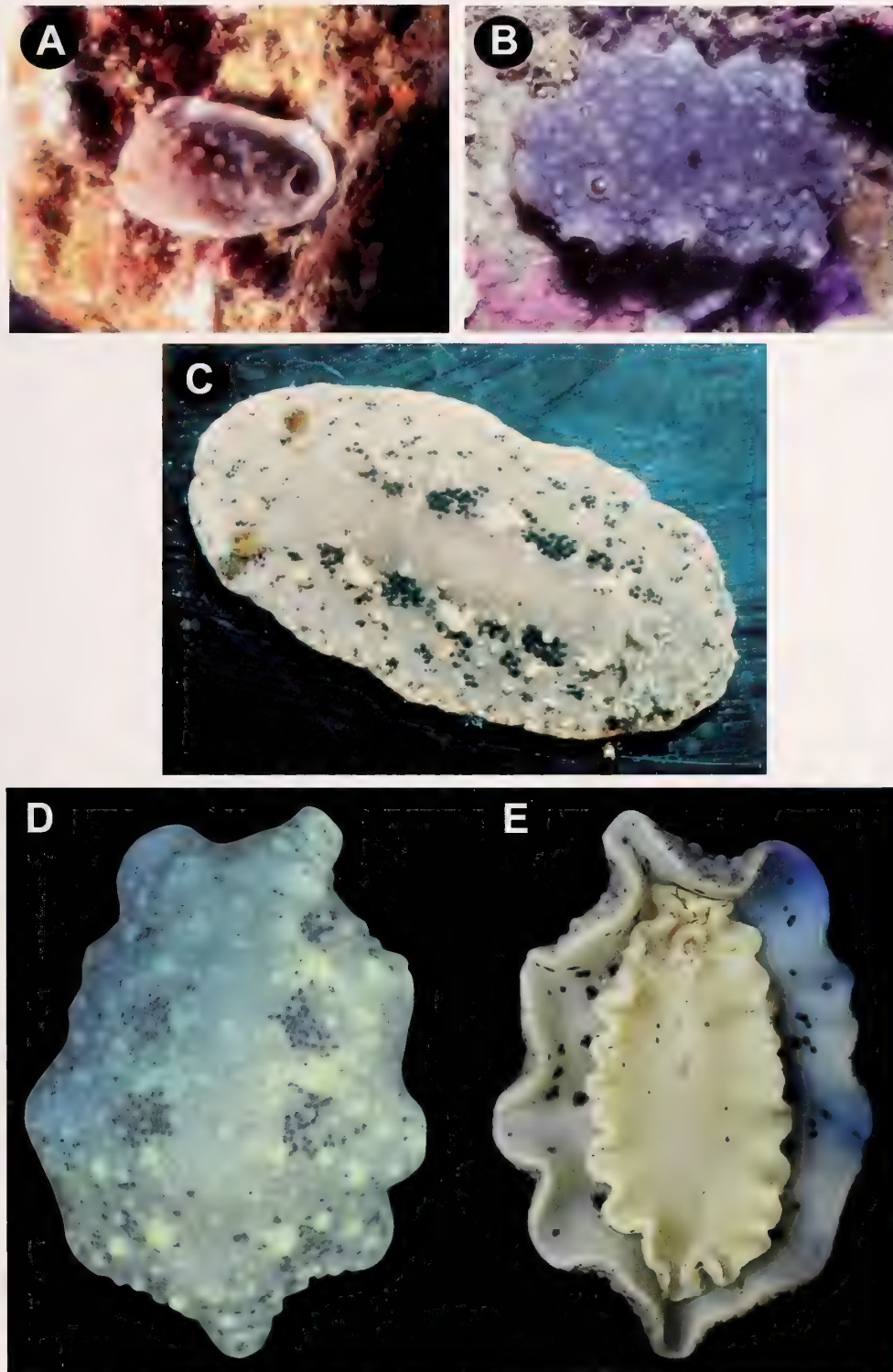


Figure 1. Living animals of *Paradoris*. A. *Paradoris multicber*, Costa Rica (INB001501499) photo by Y. Camacho-García. B. *Paradoris caeruleus* sp. nov., South Africa (CASIZ 073954) photo by T.M. Gosliner. C. Living animal of *Paradoris lopezi*, Galápagos Islands (LACM 71-45) photograph by D.K. Mulliner. D. Dorsal view of a preserved animal of *Paradoris lopezi* (CASIZ 105978) photograph by M. Zúñiga. E. Ventral view of a preserved animal of *Paradoris lopezi* (CASIZ 105978) photograph by M. Zúñiga. Note: In fig. 1D, E, the blue color on the pictures is due to an accidental stain of the specimen with methylene blue.

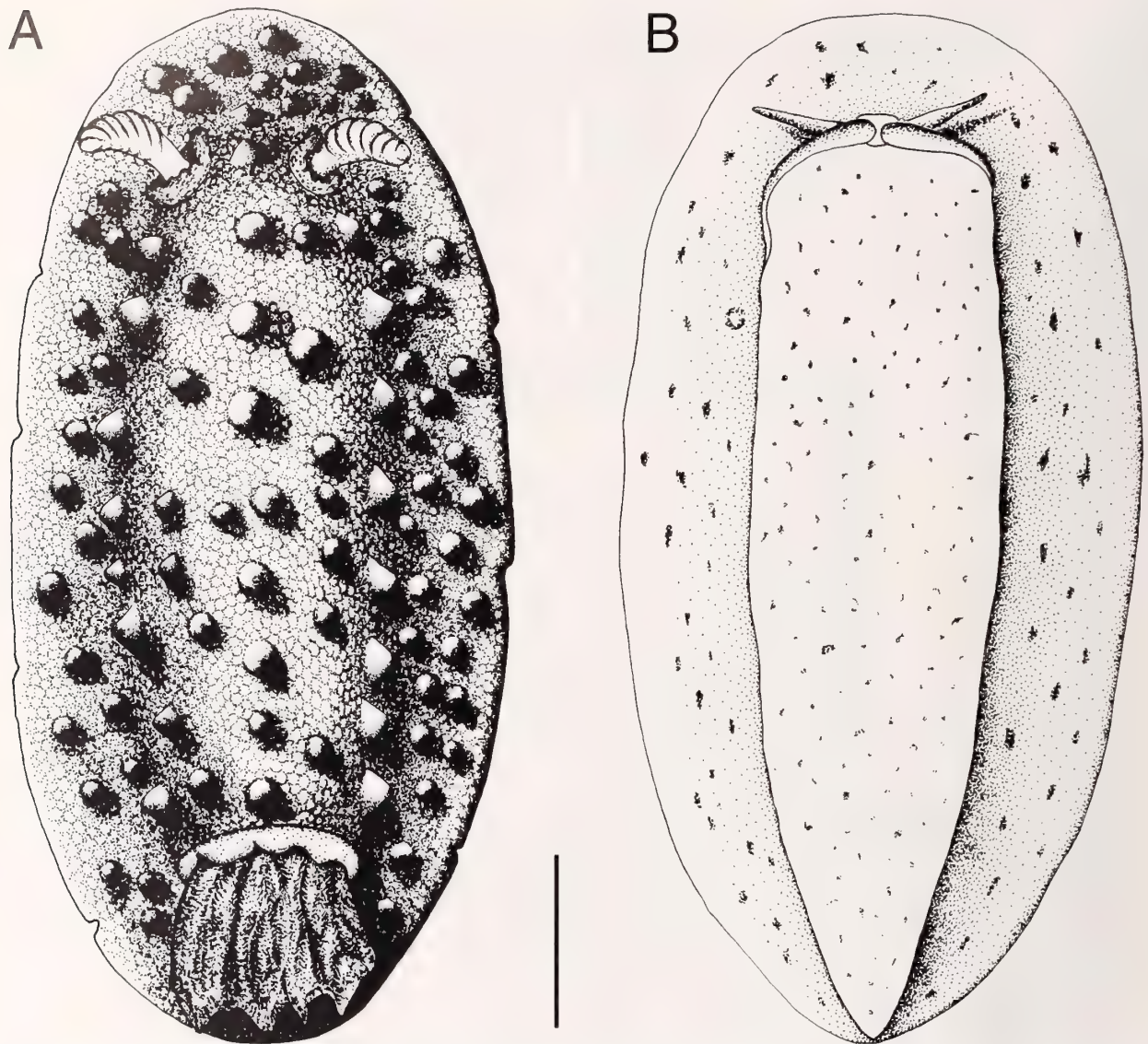


Figure 2A. Dorsal view of a preserved animal of *Paradoris multicber* from Limón, Caribbean coast of Costa Rica (INB001501499). B. Ventral view; scale bar = 5 mm.

Atlantic coast of the Americas. The original description of this species (in the genus *Percumas*) was a brief description, later expanded by Marcus (1976). The specimens examined here are identical to those described by Marcus (1970, 1976), and there is no detectable variation among the specimens. The only differences between Marcus's descriptions and ours (also pointed out by Dayrat, 2006) are that the prostate is larger in the original description than that found in the present material, the branchial sheath of our specimens has several undulations rather than being smooth as in Marcus's description, and the rhinophoral segments in some specimens examined here have one or two tubercles on each side.

A drawing of the reproductive system of a specimen from the Caribbean made by Vinicius Padula (unpublished data) consistently shows the presence of two accessory glands and three stylets. Also, the ampulla has a U-shaped form and a long and convoluted prostate folded upon itself that is also present in the three specimens we dissected from Costa Rica. The only difference found in the reproductive system of the specimen from the Caribbean that differs from ours and that of Marcus (1976) is that the duct that leads from the seminal receptacle joins the duct from the vagina before it enters into the bursa copulatrix.

Ortea (1995) stated that *P. indecora* is possibly an amphiatlantic species and that *P. multicber* is a junior

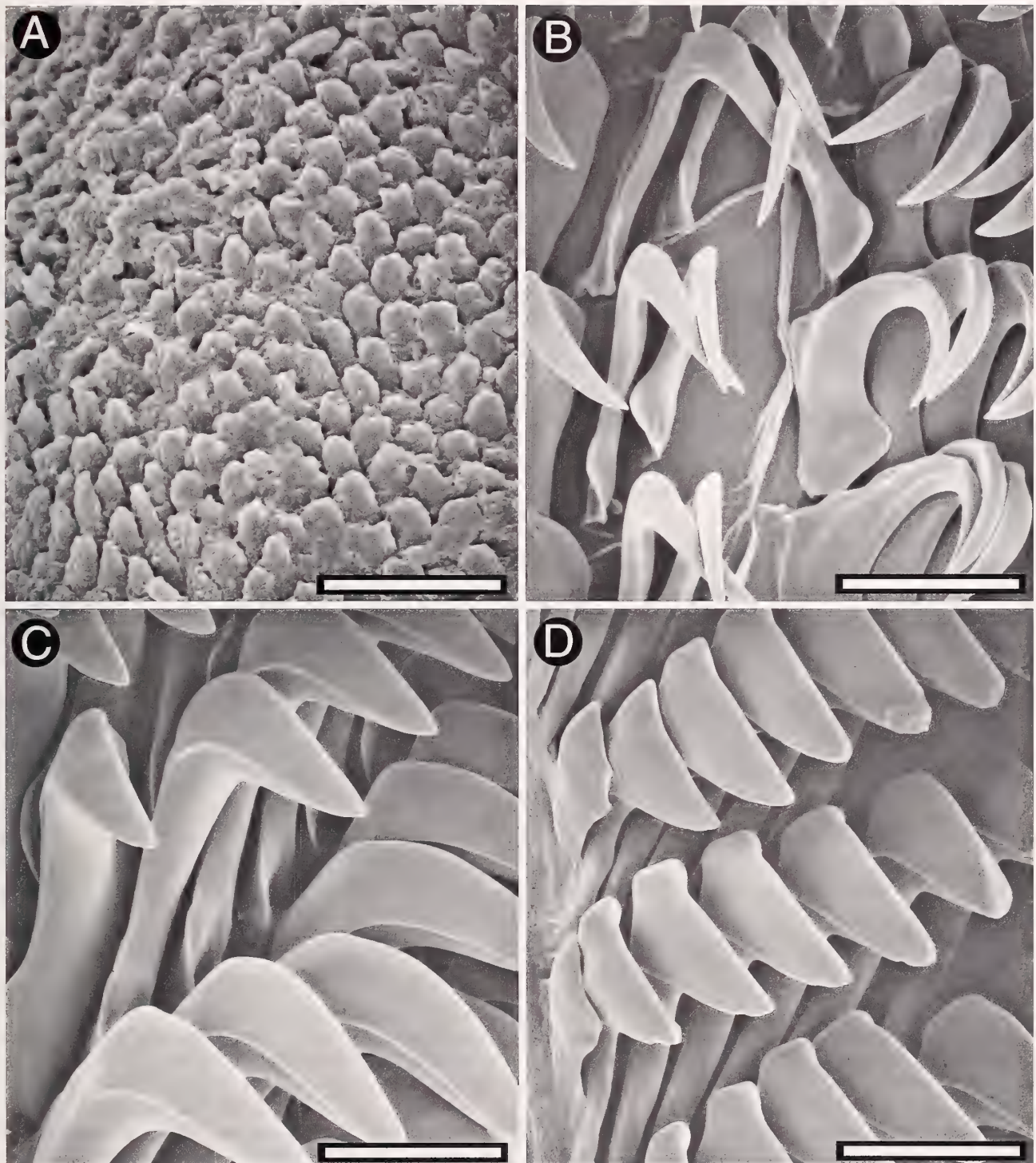


Figure 3. Scanning electron micrographs of *Paradoris multicber* (INB001501499). A. Jaw elements, scale bar = 25 μm . B. Innermost radular teeth, scale bar = 75 μm ; C. Mid-lateral radular teeth; scale bar = 75 μm . D. Outermost radular teeth scale bar = 75 μm .

synonym of *P. indecora*. Dayrat (2006) concluded that “the differences between *multicber* and *indecora* are slight” and that *multicber* and *indecora* cannot be distinguished from each other. Despite these slight

differences, and considering the geographical range of the species, Dayrat agreed to keep these species as two valid species. Based on the new specimens we examined from Costa Rica, we conclude that these two species

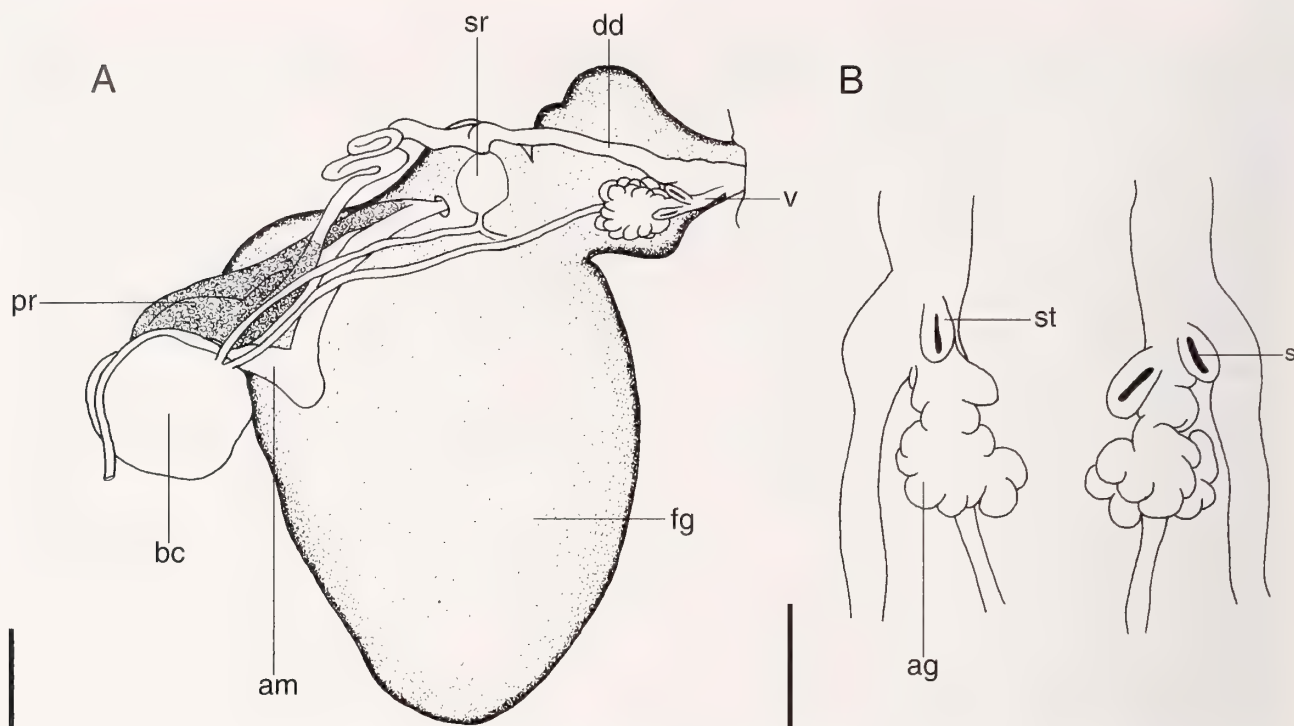


Figure 4A. Reproductive system of *Paradoris multicber* (INB001501499), scale bar = 18 mm. B. Detail of the reproductive system (INB001501499), scale bar = 23 mm; Abbreviations: ag = accessory gland, am = ampulla, bc = bursa copulatrix, dd = deferent duct, fg = female gland, pr = prostate, s = stylet, sr = seminal receptacle, st = stylet sac, v = vagina.

are distinct (Table 1) based on several anatomical differences. For example, in these specimens, and that which V. Padula examined from the Caribbean, there are consistently two accessory glands with three stylets. *Paradoris indecora* has only one accessory gland and a maximum of three stylets (Dayrat, 2006). Also, *P. indecora* has fewer, smaller tubercles arranged in two mid-dorsal lines (see description by Valdés, 2002, and Ortea, 1995:fig. 2) while those of *P. multicber* are larger, more numerous, and more evenly distributed over the entire dorsum (Figure 2).

Paradoris lopezi Hermosillo & Valdés, 2004

(Figures 1C–E, 5A, B, 6A–D, 7A, B)

Type material examined: Holotype: Punta de Pichilingue, Baja California Sur, La Paz, Mexico. (24°21'25"N, 105°33'88"W), 31 October 2004, 1 specimen (previously dissected), 32 mm preserved length, collected under coral rubble at 1 m depth, *leg.* A. Hermosillo (CASIZ 171661).

Other material examined: Punta Espinosa, Isla Fernandina, Galápagos Islands, Ecuador, 16 September 1974, 1 specimen, 71 mm preserved length, collected in the intertidal rocky shore under rocks, *leg.* G. H. Wellington (CASIZ 117625); Punta Espinosa, Isla

Fernandina, Galápagos Islands, Ecuador, 16 September 1974, 3 specimens (dissected for this study) 26–61 mm preserved length, collected in the intertidal rocky shore under rocks, *leg.* G. H. Wellington (CASIZ 105978); Darwin Research Station, Academy Bay, Santa Cruz Island, Galápagos Islands, Ecuador (0°45'06"S, 90°15'38"W), March 1971, 1 specimen, 25 mm preserved length, collected between 1–3.3 m depth, *leg.* Ameripagos Expedition (LACM 71-45).

Geographic range: This species is known only from Baja California Sur and Bahía Banderas, México, and the Galápagos Islands (present study).

External morphology: The dorsum is covered with numerous, semispherical tubercles of different sizes arranged regularly (Figures 1C, 5A). Generally, the largest tubercles are located near the center. There are no tubercles located on the rhinophoral or branchial sheaths in any of the specimens. The gill is composed of six tripinnate branchial leaves, and the rhinophores have 18–20 lamellae in a 36 mm preserved length specimen (CASIZ 105978). An SEM of the notum (not included here) clearly shows the presence of mantle holes. The margin of the mantle is wide and undulating. The anterior border of the foot is grooved and notched (Figure 5B). The oral tentacles are conical and grooved.

The background color of the living animals is gray

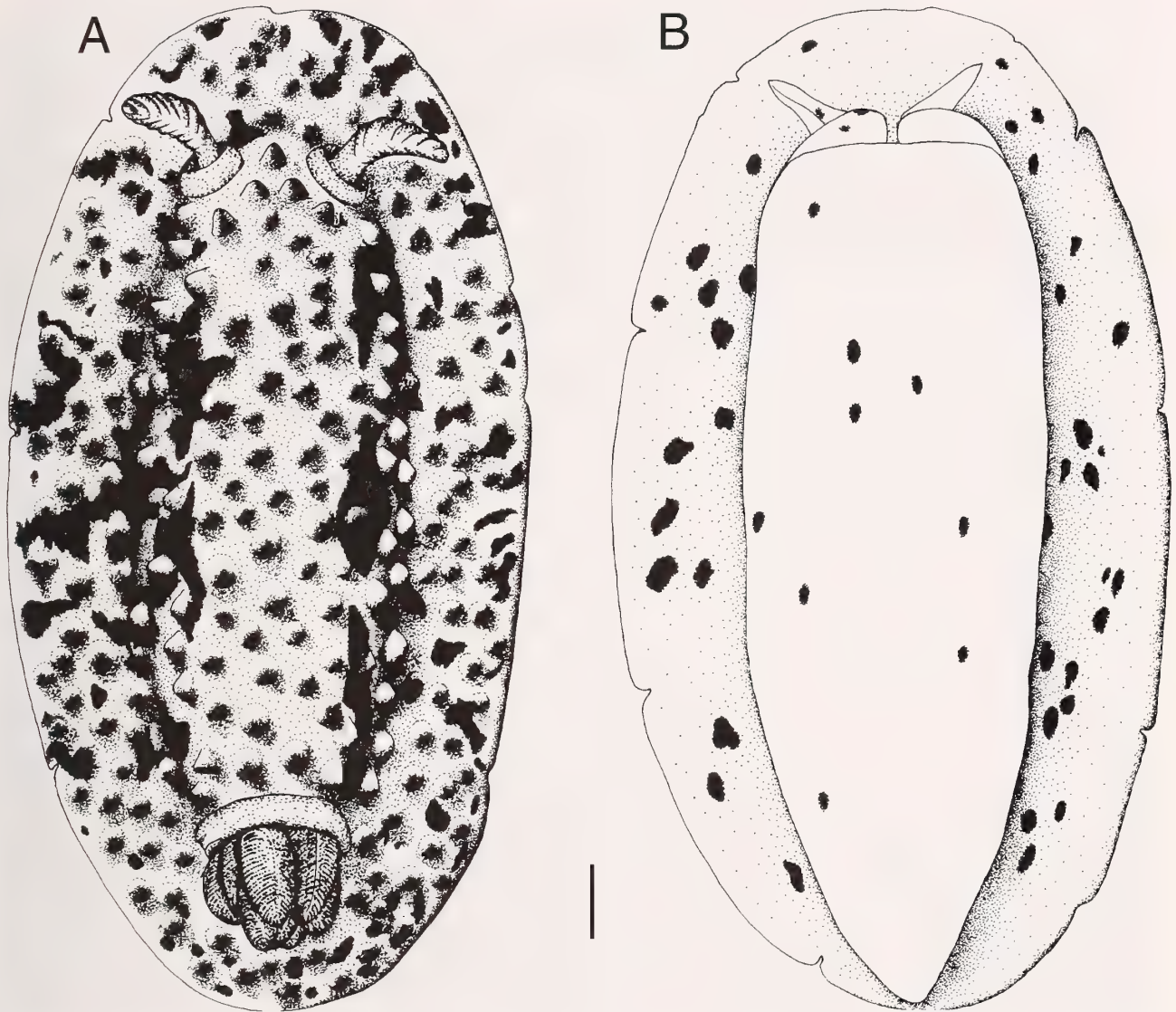


Figure 5A. Dorsal view of a preserved animal of *Paradoris lopezi* (CASIZ 117625) from Punta Espinosa, Galápagos Islands, Ecuador. B. Ventral view, scale bar = 5 mm.

with numerous small brownish orange spots arranged very densely on the entire dorsum (Figure 1C). The gray color is darker towards the middle of the dorsum. The tubercles have a pale gray base and an orange tip. There are several large black patches (one specimen has eight) composed of an aggregate of small black specks. There are simple black and brown spots near the margin of the mantle as well. Opaque white spots are also present all over the dorsum. The rachises of the branchial leaves are dark gray with small brown spots, the tips being yellowish. The foot is pale gray spotted with brown. The color of the ventral side of the mantle is pale gray with some dark brown spots. These spots are larger than those on the

foot and are arranged irregularly (Figures 1E, 5B). The rhinophores are light brown with small darker brown spots.

Anatomy: The radular formula is $42 \times (22.0.22)$ in a 35 mm preserved length specimen and $55 \times (26.0.26)$ in a 61 mm preserved length specimen. The radula is very elongated and the labial cuticle has three pieces. Jaw elements are arranged regularly (Figure 6A) (CASIZ 105978). The innermost teeth are larger, more angular, and more pointed than the rest (Figure 6B). The midlateral teeth are hook-shaped and pointed (Figure 6C). Generally, the teeth have a prolongation on the upper side that is strongest in the outer teeth.

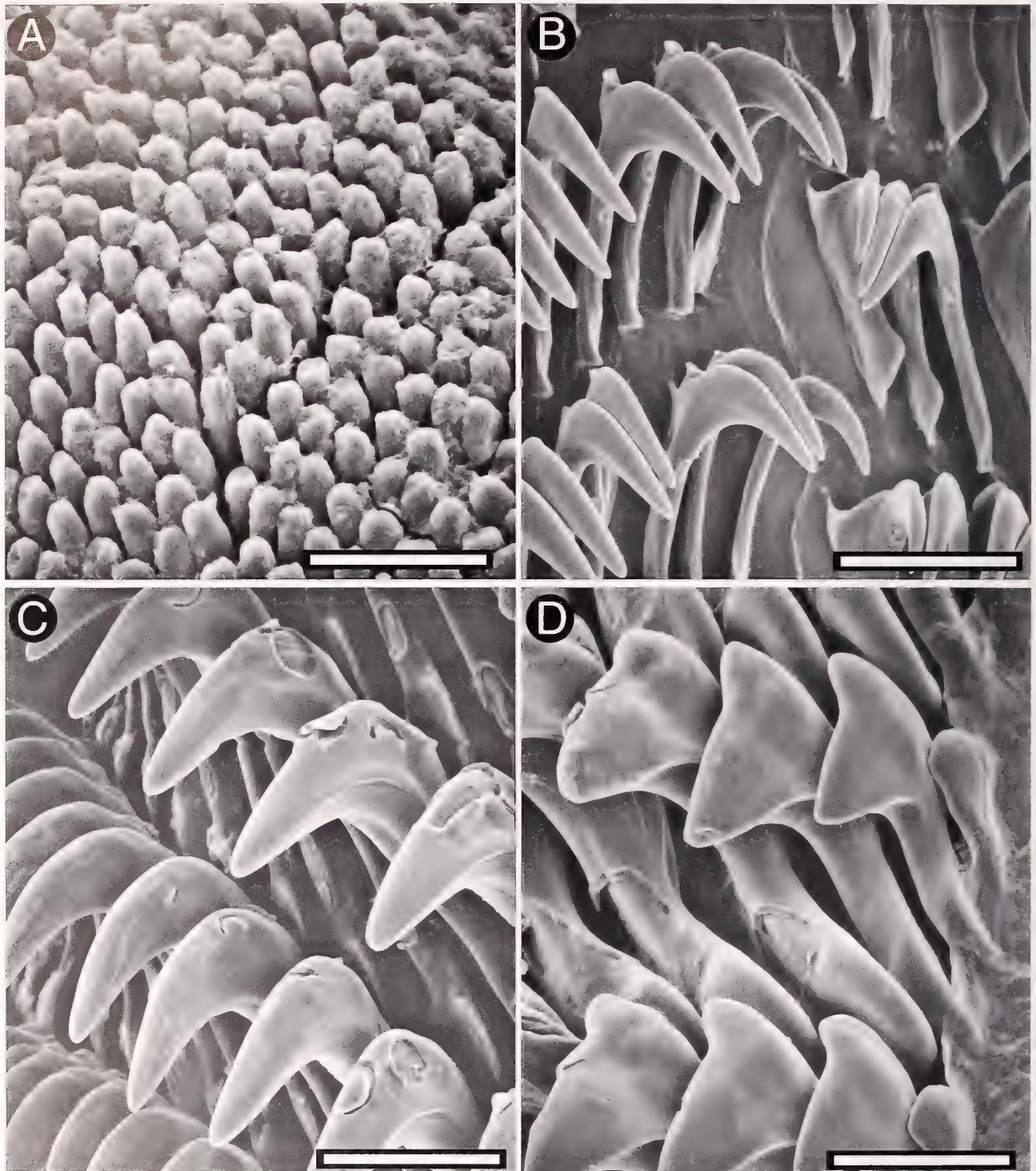


Figure 6. Scanning electron micrographs of *Paradoris lopezi* (CASIZ 117625). A. Jaw elements, scale bar = 25 μ m. B. Innermost radular teeth, scale bar = 75 μ m; C. Mid-lateral radular teeth, scale bar = 75 μ m. D. Outermost radular teeth, scale bar = 75 μ m.

There is not a sharp distinction between the base and the cusp in the outermost teeth (Figure 6D).

The ampulla is long, wider in the middle, and folded upon itself. It has a long duct located distally, prior to

its bifurcation into the oviduct and deferent duct. There is a large and convoluted prostate (Figure 7A). The deferent duct gradually narrows before ending in a short, unarmed penial section. The vagina is long

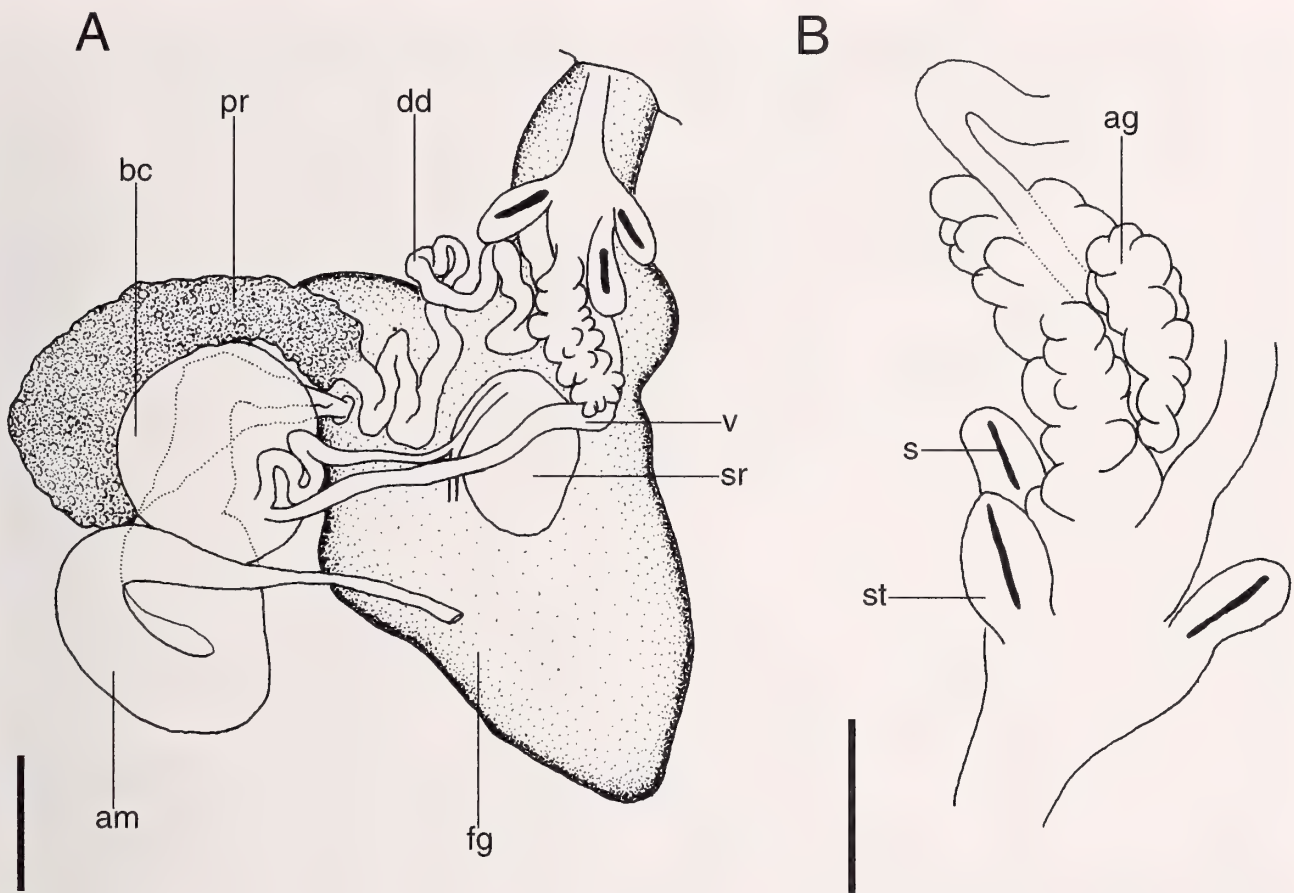


Figure 7A. Reproductive system of *Paradoris lopezi* (CASIZ 117625), scale bar = 18 mm. B. Detail of the reproductive system (CASIZ 117625), scale bar = 23 mm. Abbreviations: ag = accessory glands, am = ampulla, bc = bursa copulatrix, dd = deferent duct, fg = female gland, pr = prostate, s = stylets, sr = seminal receptacle, st = stylet sac, v = vagina.

and connects with two accessory glands and three muscular sacs, each containing a single stylet about 0.9 mm in length. The glands and the sacs are both located on the dorsal side (Figure 7B). The bursa copulatrix is pale cream, semispherical, and twice the size of the seminal receptacle. There is a convoluted duct that leads from the bursa copulatrix to the oval seminal receptacle and to the uterine duct.

Remarks: Dayrat (2006) found some differences in the original description of the species when reexamining the type material. For example, the oral tentacles were grooved (Dayrat, 2006) instead of not grooved (Hermosillo & Valdés, 2004), and there were two accessory glands and three stylet sacs (Dayrat, 2006) instead of just one stylet sac and two accessory glands (Hermosillo & Valdés, 2004). The three specimens we examined from the Galápagos Islands are in complete agreement with the description provided by Dayrat (2006). However, we also observed some morphological differences between the holotype from Mexico and the

three specimens from Isla Fernandina, Galápagos. The specimen designated as the holotype has higher tubercles (about 1.3 mm), and smaller and lighter spots on the hyponotum and notum. On the other hand, the specimens from Isla Fernandina have lower tubercles and bigger and darker spots on the hyponotum and notum.

There are several morphological differences between *P. lopezi* and *P. multiciber*. In *P. lopezi*, there are long black patches clearly visible all over the dorsum, and single black and brown-orange spots close to the margin of the mantle (Figure 1C), whereas no dark pigmentation is present on the dorsum or mantle in *P. multiciber* (Figure 1A). Also, while the foot of *Paradoris multiciber* has more but smaller dark spots than the hyponotum (Figure 2B), *P. lopezi* has fewer but larger dark spots on both the foot and hyponotum (Figure 1E). The tubercles present on each side of the rhinophoral sheaths in *P. multiciber* are not present in any of the specimens examined of *P. lopezi*. *Paradoris indecora* (Bergh, 1881) from the Mediterranean differs from *P. lopezi* by the external coloration and the mid-dorsal position of the tubercles.

Paradoris dubia, described by Bergh (1904), is also easily distinguished from *P. lopezi* by the white color of the body with dark brown spots, the translucent color of the foot, the smooth dorsum, and the lack of accessory glands and stylets. *Paradoris tsurugensis* (Baba, 1986, 1989) from Japan differs slightly from *P. lopezi* in external morphology and coloration (see Hermosillo & Valdés, 2004); for example, *P. lopezi* has more stylet sacs (Table 1) but fewer teeth ($[42 \times [22.0.22]]$) than *P. tsurugensis* ($90 \times [20-25.0.20-25]$) in specimens of comparable size.

We agree with Dayrat (2006) that the presence of dark red tubercles on the dorsal notum is probably a good character to distinguish *P. lopezi* from the rest of the species of the genus *Paradoris*, such as *P. araneosa*, *P. liturata*, and *P. erythraeensis*.

Paradoris caeruleus, new species

(Figures 1B, 8, 9)

Type material: *Holotype*: Phillips Reef, Algoa Bay, Indian Ocean coast, Cape Province, South Africa, February 1984, 1 specimen (dissected for this study) 25 mm preserved length, collected at 10–15 meters depth by SCUBA diving, *leg.* WR. Liltved (SAM A36019); *Paratype*: Phillips Reef, Algoa Bay, Indian Ocean coast, Cape Province, South Africa, May 18, 1984, 1 specimen (dissected for this study) 24 mm preserved length, *leg.* WR. Liltved (CASIZ 073954), with two microslides.

Geographic range: This species is known only from South Africa (present study).

External morphology: The body is oval and elongated, higher in the middle portion. The dorsum is covered with numerous low tubercles of various sizes closely arranged and densely distributed. Wider tubercles are surrounded by smaller ones. There are no larger tubercles located on the rhinophoral sheaths as in *P. multicir*. There are numerous large holes covering the surface of the notum. The gill is composed of seven tripinnate branchial leaves, and the rhinophores have 10 lamellae in a 24 mm preserved length specimen (SAM A36019). The number of lamellae and branchial leaves in the other specimen available are not provided since these structures were retracted in their sheaths. The mantle is wide and undulating. The anterior border of the foot is grooved and notched (Figure 9A). The oral tentacles are finger-like in shape and grooved. The foot is completely covered by the notum when the animal is in motion.

The background color of living animals is a uniform gray blue with two black spots (Figure 1B) located almost halfway between the rhinophores and the branchial leaves; however, there are also some small

spots present around the margins of the notum. Around the larger and smaller tubercles, there is an aggregation of minute white spots that are also present along the mantle margins. The branchial leaves and the base of the rhinophores are brownish black in color, while the tips of the rhinophores are white.

The ventral side of preserved specimens is cream. The foot has several brown spots along the external margin that are also present on the hyponotum. However, there are no spots present on the sole of the foot. The oral tentacles are lightly speckled with brown.

Anatomy: The radular formula of a 25 mm long specimen is $50 \times (21.0.21)$ (SAM A36019) and a 23 mm long specimen is $38 \times (21.0.21)$ (CASIZ073954). The jaw elements are arranged regularly in three discrete pieces (Figure 8A). The teeth are strong, smooth, and slender. The innermost teeth are less angular and pointed than in the other species (Figure 8B). The midlateral teeth are hook-shaped and pointed (Figure 8C). The outermost teeth do not have the prolongation on the upper side or cusp sometimes present in other species of *Paradoris* (Figure 8D).

The ampulla is short, tubular, and convoluted in the middle section, and it branches into a short oviduct and the prostate. The oviduct enters the female gland mass distally. The thick and convoluted deferent duct leads to a short and granular prostate (Figure 9B). The deferent duct opens into a common atrium with the vagina. The penis is unarmed. There is a pair of highly ramified accessory glands and two muscular sacs containing two stylets each. The glands and the sacs are located on the dorsal side (Figure 9C). Each stylet is about 0.2 mm in length. The short vagina connects to a large and oval bursa copulatrix. From the bursa copulatrix leads another short duct that connects to the seminal receptacle and the short uterine duct. The bursa copulatrix is about five times larger than the seminal receptacle.

Etymology: From the Latin “*caeruleus*” in reference to the blue color of the species.

Remarks: Dayrat (2006) described specimens from the Cape Province of South Africa that he attributed to *Paradoris erythraeensis* (Vayssière, 1912). These animals differ from the holotype of *P. erythraeensis* in several important aspects of their anatomy. The holotype of *P. erythraeensis* has a series of conical tubercles on the back. Gohar & Abu-Ela (1959) also noted these tubercles in another specimen they examined from the Red Sea. They also described the color of the living animal as “light gray with scattered roundish or irregularly shaped blackish brown patches. It is finely tuberculated, large tubercles occurring in the centre of the black patches and surrounded by more

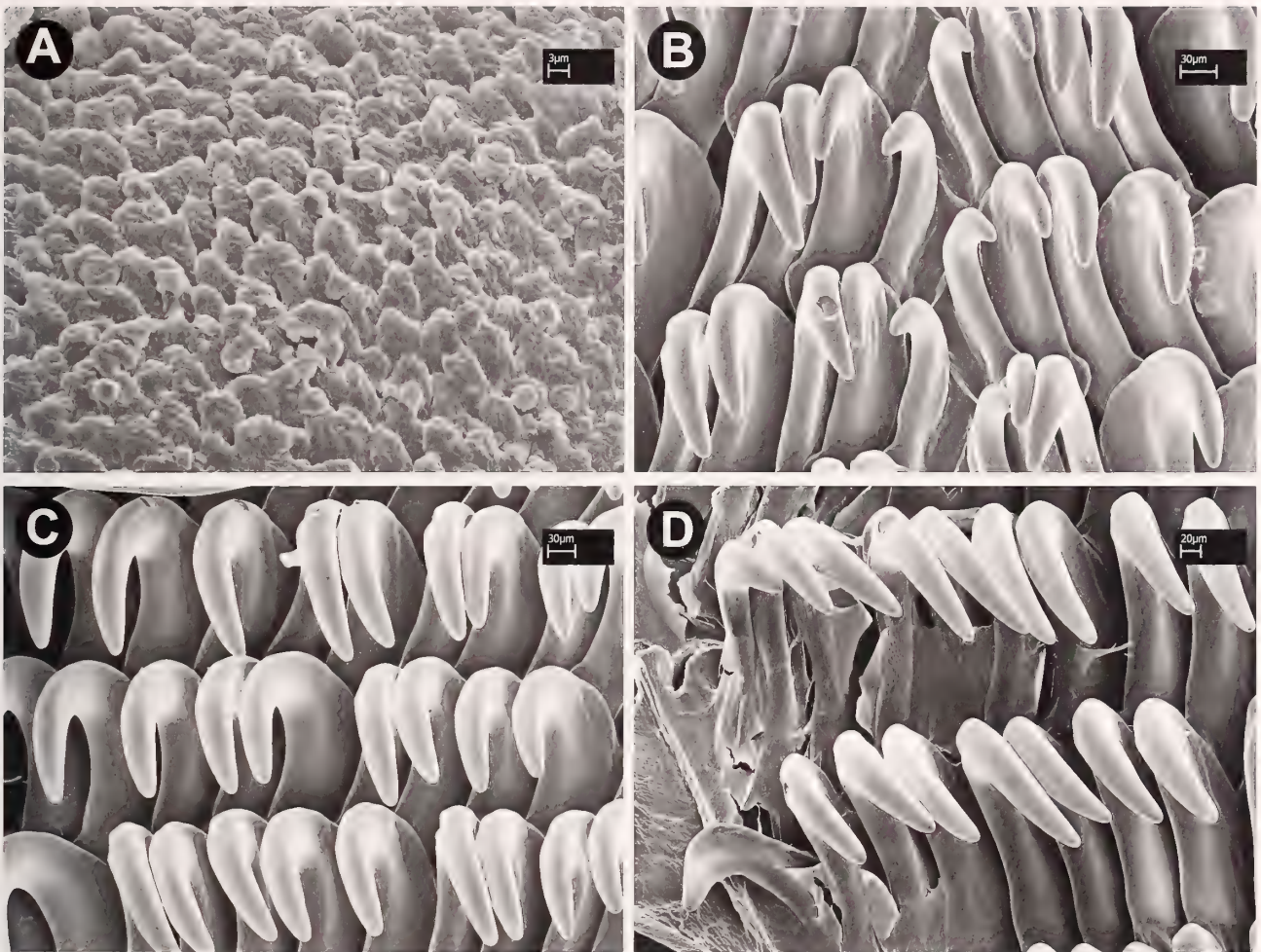


Figure 8. Scanning electron micrographs of *Paradoris caeruleus* sp. nov. (SAM A36019). A. Jaw elements. B. Innermost radular teeth. C. Mid-lateral radular teeth. D. Outermost radular teeth.

numerous smaller ones.” In contrast, the specimens from South Africa that Dayrat examined are white with black spots and have a granular notum without any tubercles. Dayrat noted that the radular teeth of specimens of *P. erythraeensis* have a hook-shaped spur on the base of the outermost teeth, and that the shape of the outer radular teeth of the specimens from South Africa could not be determined, because the slides containing the radulae had dried out. We remounted these two radulae, and the outermost teeth lack a basal spur on the outer tooth in both specimens. Dayrat noted that the holotype of *P. erythraeensis* has two simple accessory glands and a single elongate stylet sac, and that no glands or stylet sacs could be found in one of the South African specimens (A32370). He did not mention the second South African specimen (A35586). This specimen does have the vestibular glands and stylet sacs present with other portions of the reproductive system in the previously dissected animal.

There are two ramified accessory glands and two stylet sacs, although no stylets were visible with the sacs.

Based on his examination of specimens of *Paradoris* from the Indian and Pacific Oceans, he concluded that all of these specimens should be considered as *P. erythraeensis*, although he did state that these may actually represent a species complex. His criterion for uniting these specimens was the presence of an elongate duct of the receptaculum seminis, and he concluded that all other features, including the texture of the notum, body color, radular tooth shape, and number and shape of accessory glands and stylets, represented intraspecific variation. Another interpretation of this variation can be made. For example, the three specimens attributed to *P. erythraeensis* from Tanzania all have a smooth notum, a pinkish tan color with mottled darker areas, and two ramified accessory glands with one or two stylet sacs. In other words, combining species solely on the basis of having a long receptacu-

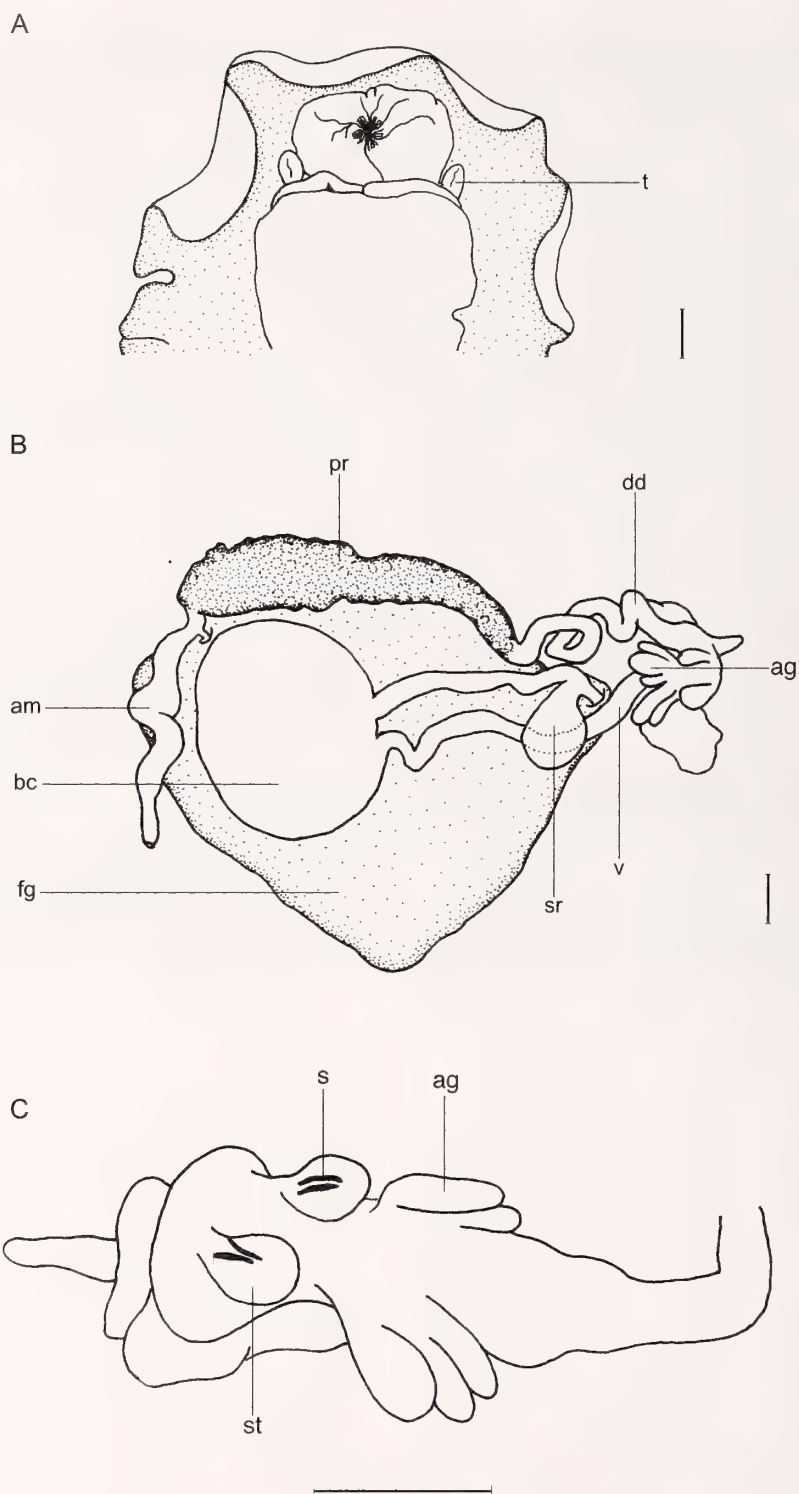


Figure 9A. Ventral view of the mouth area, scale bar = 1 mm. B. Reproductive system of *Paradoris caeruleus* sp. nov. (SAM A36019), scale bar = 1 mm. C. Detail of the reproductive system (CASIZ 117625), scale bar = 1 mm. Abbreviations: ag = accessory glands, am = ampulla, bc = bursa copulatrix, dd = deferent duct, fg = female gland, pr = prostate, s = stylets, sr = seminal receptacle, st = stylet sac, t = tentacle, v = vagina.

Table 1
Comparative morphology of the valid species of the genus *Paradoris*.

Species	Description source	Distribution	Dorsal color	Ventral color in preserved animals	Middle part of the notum	Rhinophoral sheaths	Branchial leaves	Prostate	Accessory Glands	Stylets	Radula
<i>Paradoris indecora</i> (Bergh, 1881)	Valdés, 2002 and Dayrat, 2006	Mediterranean and eastern Atlantic ocean	light gray to light cream or whitish with a pale brown tinge in the center. Several small brown spots on tips of tubercles and small opaque white dots	whitish with or without dark dots	covered with small, rounded tubercles. The largest ones occur in two lines	with tubercles	8 tripinnate leaves	tubular, divided into two portions	1 (Valdés, 2002); a maximum of 2 (Dayrat, 2006)	2 (0.4 mm) (Valdés, 2002); a maximum of 3 (Dayrat, 2006)	56 × (23/24.0.23/24) 34 mm long specimen
<i>Paradoris dubia</i> (Bergh, 1904)	Miller, 1995 and Dayrat, 2006	South-western Pacific Ocean (from New Zealand to South Australia) and south-eastern Indian Ocean (Western Australia)	white body with dark reddish brown spots and light gray spots on tips of tubercles	creamish with or without brown spots	with tubercles all over	smooth or with crenulate edge	up to 8 tripinnate leaves	tubular in U-shaped or convoluted	lacks accessory gland	absent	37 × (16.0.16) 15 mm long specimen
<i>Paradoris liturata</i> (Bergh, 1905)	Dayrat, 2006	Papua New Guinea and Indonesia	light greyish to whitish with a network of black longitudinal and/or transversal lines	—	with tubercles of various sizes surrounded by a network of black lines	smooth	up to 8 tripinnate leaves	flattened, divided into two portions	up to 4 accessory glands	2 (0.56–0.82 mm)	45 × (17.0.13) 16 mm long specimen
<i>Paradoris erythraeensis</i> (Vayssières, 1912)	Dayrat, 2006	Djibouti, Suez Canal, Red Sea, Tanzania, South Africa, Thailand, Indonesia and the Philippines	white or yellowish to pink-tan with brown spots	whitish sometimes with brown dots	smooth or with tubercles	smooth	6 tripinnate leaves	flattened, divided into two portions	2	2 (0.32–0.42 mm)	37 × (15.0.15) 14 mm long specimen
<i>Paradoris mulcheri</i> (Marcus, 1970)	present study	Brazil and Costa Rica	light brown to pale cream scattered with numerous small dark brown spots composed of an aggregate of brown points	white with dark spots arranged separately	the largest tubercles located in the middle	some specimens with 1–2 tubercles at each side	6 tripinnate leaves	very large, and folded into itself	2	3 (0.5 mm)	55 × (18.0.18) 18 mm long preserved specimen; 47 × (16.0.16) 40 mm long preserved specimen
<i>Paradoris tsuringensis</i> (Baba, 1986)	Baba, 1986; Baba, 1989 and Dayrat, 2006	Japan	faintly grayish yellow or grayish brown scattered with blackish brown flecks	covered with chocolate spots	with tubercles speckled with chocolate brown at the base	smooth	6 tri or quadripinnate leaves	very large, discrete and massive	2 (1 mm)	2 (1 mm)	90 × (20–25.0.20–25) 50 mm long specimen
<i>Paradoris araneosa</i> (Valdés, 2001)	Valdés, 2001	New Caledonia (deep-sea)	pale brown with dark brown spots and numerous small darker dots. Larger tubercles opaque white	covered with rounded tubercles except in those areas with a number of small depressions	covered with rounded tubercles except in those areas with a number of small depressions	—	6 tripinnate leaves	flattened and granular, divided into two portions	1 or 2	2 (0.3 mm)	68 × (16.0.16) 32 mm long preserved specimen
<i>Paradorislopezi</i> (Hermosillo & Valdés, 2004)	present study	Mexico and Galapagos Islands	gray with small dark brown-orange spots. Several big black spots composed of an aggregate of small black points	pale gray with brown spots larger than those in the foot	the largest tubercles located in the middle	smooth	6 7 tripinnate leaves	granular and convoluted	2	3 (0.9 mm)	42 × (22.0.22) 35 mm long preserved specimen; 55 × (26.0.26) 61 mm long preserved specimen
<i>Paradoris caeruleus</i> sp. nov.	present study	South Africa	gray blue with some black spots. Tubercles surrounded by an aggregate of minute white spots	cream	covered with low tubercles of different sizes. Wider tubercles surrounded by small ones	smooth	7 tripinnate leaves	short and granular	1	4 (2 styles in each sac)	50 × (21.0.21) 25 mm long specimen; 38 × (21.0.21) 23 mm long preserved specimen

— No information available

lum duct may not be the most precise way to determine distinct taxa. Rather, looking for correlations of characters appears to have produced a better estimation of species boundaries and diagnostic characters. When these practices are employed, it appears that the South African specimens share several characters not found in other specimens attributed to *P. erythraeensis* by Dayrat. Namely, the two specimens from South Africa both have a smooth body, white body color with black spots, outer radular teeth without a basal spur, and are distinct from all other material examined. We consider these specimens to represent a distinct, undescribed species. This conclusion is further reinforced by the fact that the South African specimens are found in both warm and cold waters of the Cape Peninsula, a region with an extremely high level of endemism and relatively few Indo-Pacific species (Gosliner, 1987). The rest of the specimens considered *P. erythraeensis* by Dayrat are from strictly tropical regions of the Indo-Pacific.

Paradoris caeruleus differs from the rest of the species of the genus *Paradoris* by its gray blue dorsal color with black spots. Also, the radular teeth are much finer than those found in other species. In most species of the genus *Paradoris* (with the probable exceptions of *P. dubia* and the specimens from South Africa that Dayrat attributed to *P. erythraeensis*), the outer teeth are smaller and have a short triangular cusp, and the outermost tooth is sometimes reduced to a simple plate (see Dayrat (2006) for comparison). In *P. caeruleus*, there is a prolongation of the outer teeth that is not present in most of the species of the genus. It also differs in its reproductive anatomy in that it is the only species known to have two stylets in each of two stylet sacs.

Paradoris caeruleus will be compared in detail to the South African specimens that Dayrat included in *P. erythraeensis* and that we consider as representing a distinct, undescribed species (see above). *Paradoris caeruleus* has a notum that bears regular rounded tubercles evenly distributed over most of the surface of the notum, while the notum of *P. sp.* is granular in texture and devoid of tubercles. The body color of *P. caeruleus* is blue with two black spots on the notum, situated between the rhinophores and gill. Minute opaque white spots are found at the base, covering the tubercles and surrounding their base. In contrast, *P. sp.* is white with a few small scattered black spots and evenly scattered smaller opaque white spots. The number of radular teeth per half-row differs consistently, based on examination of the two specimens of each species. In *P. caeruleus*, there are 21 teeth per half-row, while in *P. sp.* there are 15 and 16 teeth per half row. Perhaps even more importantly, all of the teeth of *P. caeruleus* have rounded apices, while those of *P. sp.* are more acutely pointed. This is not an artifact of

wear, as all teeth in the radula, whether old or newly formed have these distinctive shapes. Both species have two ramified accessory glands, but there are more ramifications in the glands of *P. caeruleus* than in *P. sp.* Both species have a pair of stylet sacs, but each sac of *P. caeruleus* had two stylets, while no stylets were found in the sacs of *P. sp.* Finally, the receptaculum duct of *P. caeruleus* is relatively short, while that of *P. sp.* is elongate. While the sample size for both species is relatively small, with only two individuals each, the number and degree of difference warrants separating them as distinct species. The description of *P. sp.* will be published in a separate paper that reviews it together with several other species that were considered *P. erythraeensis* by Dayrat.

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New Species of the Genus *Caelatura* Conrad, 1865 (Mollusca, Gastropoda, Barleeidae) from off the Brazilian Coast

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Abstract. Six new species of barleeid gastropods of the genus *Caelatura* are described from the Brazilian continental shelf. *Caelatura albertoi* n. sp. occurs off the states of Amapá and Pará (67–173 m depth); *Caelatura aulakion* n. sp. is found off Amapá (160 m depth); *Caelatura noxia* n. sp. is found off Espírito Santo (20–96 m depth); *Caelatura carinata* n. sp. is found off Ceará (70 m depth); *Caelatura phrix* n. sp. is found off the state of Bahia (50–67 m depth) and *Caelatura tupi* n. sp. is found off Sergipe (25–900 m depth). These species are compared to six other *Caelatura* species previously reported from the same region. This is the first report of the genus *Caelatura* from northern Brazil.

INTRODUCTION

Barleeid molluscs of the genus *Caelatura* Conrad, 1865 are minute gastropods, about three millimeters long, that usually inhabit shallow waters of the continental shelf. They are present in most of the Western Atlantic (Ponder, 1983; Rios, 1994).

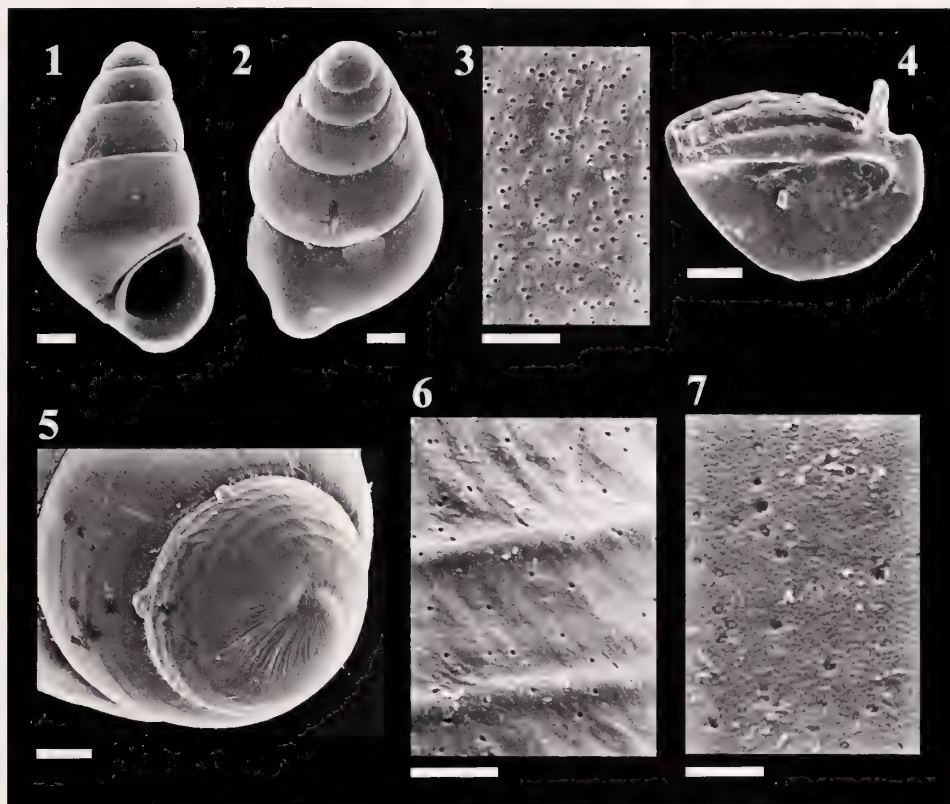
In the Western Atlantic Ocean eight species of *Caelatura* have been reported. Six of them inhabit the Brazilian coast: *C. pernambucensis* (Watson, 1886) and *C. rustica* (Watson, 1886), *C. barcellosi* Absalão & Rios, 1995 and *C. spirocordata*, Absalão & Rios, 1995 and *C. speculabunda* Absalão, 2002 and *C. tigrina* Absalão, 2002. The first two species and *C. microstoma* (Watson, 1886) were described in *Rissoa* and, subsequently reassigned to *Caelatura* by Ponder (1983). *Assimineia gerhardtae* De Jong & Coomans, 1988 was described from the Caribbean region, but Rolán & Cruz-Ábrego (1998) re-classified it to *Caelatura* based on the smooth protoconch without minute pits, the penis shape and the similar shell profile to *C. rustica* (see Rolán & Cruz-Ábrego, 1998: 5). This species is discussed with respect to *C. albertoi* n. sp. and *C. aulakion* n. sp. because all of them are devoid of conspicuous sculpture. All other species presently classified in *Caelatura* were originally described in that genus.

MATERIALS AND METHODS

The material analyzed was provided by the oceanographic expeditions GEOMAR I Amapá and Pará states (June 1965); GEOMAR II, (September 1970); by AMASSEDs, Amapá State (October 1991); by REVIZEE Program, Score Nordeste (November 2000),

and Score Central (February and April 1996; June and July 2001); PCABS – Petrobras (April 2002). The shells were observed with optical and scanning electron microscopes. Identifications were done from published descriptions (Watson, 1886; Ponder, 1983; Rios, 1994; Absalão & Rios, 1995; Absalão, 2002; Rolán & Cruz-Ábrego, 1998) and from comparison with type-material and/or original descriptions and illustrations. The descriptions were based on shell characters and discussion will be restricted to those species belonging to their specific ornamented group, e.g., smooth members of *Caelatura* will be compared only with other smooth *Caelatura*. The number of protoconch whorls was counted by the method of Leal (1991).

Abbreviations used: AMASSEDs—Multidisciplinary Amazon Shelf Sediment Study; DOUFPE—Departamento de Oceanografia, Universidade Federal de Pernambuco, Recife, Brazil; GEOMAR—Programa de Geologia Marinha do Brasil; IBUFRJ—Instituto de Biologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; MNRJ—Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil; MORG—Museu Oceanográfico “Eliézer de Carvalho Rios” da Fundação Oceanográfica do Rio Grande, Rio Grande, Brazil; PCABS—Projeto de Caracterização Ambiental da Bacia de Sergipe (Sergipe Basin Environmental Characterization Project, Petrobras Co.); REVIZEE—Programa de Avaliação do Potencial Econômico da Zona Econômica Exclusiva do Brasil; MZSP—Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil; ZMA—Zoologisch Museum Amsterdam, Amsterdam, The Netherlands. MNHN—Muséum national d’histoire naturelle, Paris, France.



Figures 1–7. *Caelatura albertoi* n. sp. Figure 1. holotype (MNRJ 10305), length 1.75 mm; Figure 2. paratype (IBUFRJ 14182), length 1.7 mm; Figure 3. detail of sculpture of teleoconch of holotype; Figure 4. operculum of a spare specimen IBUFRJ 14186; Figure 5. protoconch of paratype; Figure 6, 7. detail of protoconch of holotype, scale 5 µm. Scale bar: 1: 200 µm; 2: 100 µm; 3, 6: 10 µm; 4, 5: 50 µm; 7: 5 µm.

Systematics

Barleeidae Gray, 1857

Caelatura Conrad, 1865 Type species: *Pasithea sulcata* Lea, 1833: 124, fossil, Eocene, Alabama, USA.

Subsequent designation by Ponder (1983: 244).

Diagnosis: (based on Ponder 1967; 1983).

Shell stout, elongate-conical, usually non-umbilicate, smooth or with axial or spiral sculpture, microsculptured with irregular minute pits; protoconch paucispiral, dome-shaped, sculptured with very closely packed, minute irregular pits; operculum oval, corneous, with or without peg, eccentric nucleus.

Caelatura albertoi n. sp. (Figures 1–7)

Description: Shell conical, whorls slightly convex, light cream, opaque. Protoconch paucispiral, about 2 whorls, macroscopically smooth (Figure 5, 6–7) obsolete spiral threads. Opisthocline axial threads may be present. Pits spreading irregularly over entire protoconch. Teleoconch smooth but abundant microscopic deep pits. Suture impressed. Base slightly convex.

Aperture suboval posteriorly angled, varicose. Minute umbilical chink. Operculum ovoid, red-orange, a sulcus along inner (columellar) edge, strong longitudinal rib near columellar edge. Peg rises from most posterior part of longitudinal rib extending beyond inner edge.

Dimensions: Holotype with 3.5 whorls in teleoconch; height 1.75 mm; width 1.0 mm.

Type locality: AMASSSEDs, sta. 4134, 02°21'00"N, 48°29'00"W, 72 m, Cruise IV, leg. 1, 22/x/1991, RV "Columbus Iselim," Amapá State, off northern Brazil.

Type material: Holotype: MNRJ 10305; paratypes (five shells in each lot): IBUFRJ 14182; MNRJ 10306; MZSP 43204; MORG 41071; ZMA 4.04.046; MNHN; DOUFPE 5023. All paratypes from type locality.

Additional material: GEOMAR I, sta. 72 Am.105S, 02°51'42"N, 48°46'00"W, 86 m, 14/vi/1965, [17]; sta. 73 Am.106 03°04'18"N, 48°25'00"W, 173 m, 14/vi/1965, [1], Amapá and Pará State; GEOMAR II, sta. 72 03°04'00"N, 48°52'48"W, 13/ix/1970, 94 m, [1]; sta. 92 Am. 32 02°52'12"N, 49°19'00"W, 09/xi/1970, 65 m, [6]; sta. 124 03°32'12"N, 48°59'48"W, 13/ix/1970, 103 m,

[19]; sta. 2413 Am.134S 04°18'48"N, 05°17'06"W, 89 m., 27/ix/1970, [15]; sta. 2425 Am. 152A 03°33'12"N, 49°32'18"W, 87.4 m, 30/ix/1970, [3]; sta. 2441 Am.174S 01°46'00"N, 47°14'00"W, 10/x/1970; 77 m, [1]; all Amapá State; AMASEDS, sta. 4134, 02°21'00"N, 48°29'00"W, 72 m, 22/x/1991 [137]; sta. 4128 03°25'00"N, 49°54'00"W, 71 m, 21/x/1991, [1]; REVIZEE Central, sta. 20 19°16'05"S, 38°00'32"W, 67 m, 28/vi/2001 [17].

Etymology: This species is named for Dr. Alberto Garcia de Figueiredo Júnior, who kindly allowed us access to malacological material from the Oceanographic Operation GEOMAR I.

Distribution: Amapá to Pará, Northern Brazil (02°21'00" N to 19°16'05" S).

Remarks: As a smooth species, *C. albertoi* resembles *C. rustica* (see Ponder, 1983: 268, fig. 16a), *C. gerhardtae* De Jong & Coomans, 1988 (see Rolán & Cruz-Ábrego, 1998: 6, fig. 15) and *C. aulakion* n. sp. *Caelatura albertoi* has a stronger varix than that of *C. aulakion*, and a granulose texture on the protoconch, whereas it is smooth in the latter species. Also, *C. aulakion* has a peripheral furrow between the body whorl and the base, whereas *C. albertoi* has no such furrow. *Caelatura albertoi* can be distinguished from *C. rustica* and *C. gerhardtae* by the lack of a varix behind the aperture in the two latter species.

***Caelatura aulakion* n. sp. (Figures 8–13)**

Description: Shell conical, whorls slightly convex, cream-whitish with pale orange spots, opaque. Protoconch paucispiral, macroscopically smooth, 6–7 thin spiral threads. Pits spreading irregularly over entire protoconch. Teleoconch smooth, but microscopic, irregularly arranged deep pits. Shallow furrow present between body whorl and base. Suture impressed. Base slightly convex. Aperture suboval. Lip thin. Umbilicus lacking. Aperture varicose.

Dimensions: Holotype with 3.5 whorls in teleoconch; height 2.2 mm; width 1.25 mm.

Type locality: Amapá, 04°27'00"N, 49°58'00"W, 160 m, 13/x/2000, Amapá State, northern Brazil.

Type material: Holotype: MNRJ 10308; paratypes (three shells in each lot): IBUFRJ 14181; MNHN; MORG 41072; ZMA 4.04.045; MZSP 43205; DOUFPE 5025 All paratypes from type locality.

Etymology: *aulakion* = n. dim. from *aulax* (L.) and *-akos* (Gr.) referring to the furrow bordering the last whorl.

Distribution: Amapá State, northern Brazil.

Remarks: *Caelatura aulakion* is distinguished from *C. albertoi* as discussed for *C. albertoi*. *Caelatura aulakion* can be distinguished from *C. rustica* and *C. gerhardtae* by having a varix behind the aperture, whereas the latter two species do not. Furthermore, *C. aulakion* has irregular pits on the protoconch, whereas they are absent in both *C. rustica* and *C. gerhardtae*.

***Caelatura carinata* n. sp. (Figures 14–19)**

Description: Shell pupoid-elongate, stout, whorls angulated in median portion, yellow-orange, opaque. Protoconch hemispherical, paucispiral, macroscopically smooth. Teleoconch carinate at mid-whorl, 5 strong undulating rounded spiral cords on penultimate whorl, 7 on body whorl, 4–5 more at base. Interspaces between spiral cords deeply grooved, separated by ridges like fine granulated blades. Deep pits at top of spiral cords in somewhat linear arrangement. Width of interspaces variable, usually about same width as spiral cords. Suture impressed. Aperture suboval. Lip thin. Minute chink-like umbilicus.

Dimensions: Holotype with 3.75 whorls in teleoconch; height 1.45 mm; width 0.7 mm.

Type locality: REVIZEE NE IV sta. 130A, 4° pernada 03°20'00"S, 38°11'00"W, 71 m, 14/xi/2000, RV "Antares," northeast Brazil.

Type material: Holotype: MNRJ 10307; paratypes: DOUFPE 4938 [1]; IBUFRJ 14179 [1]; DOUFPE 4907 [1].

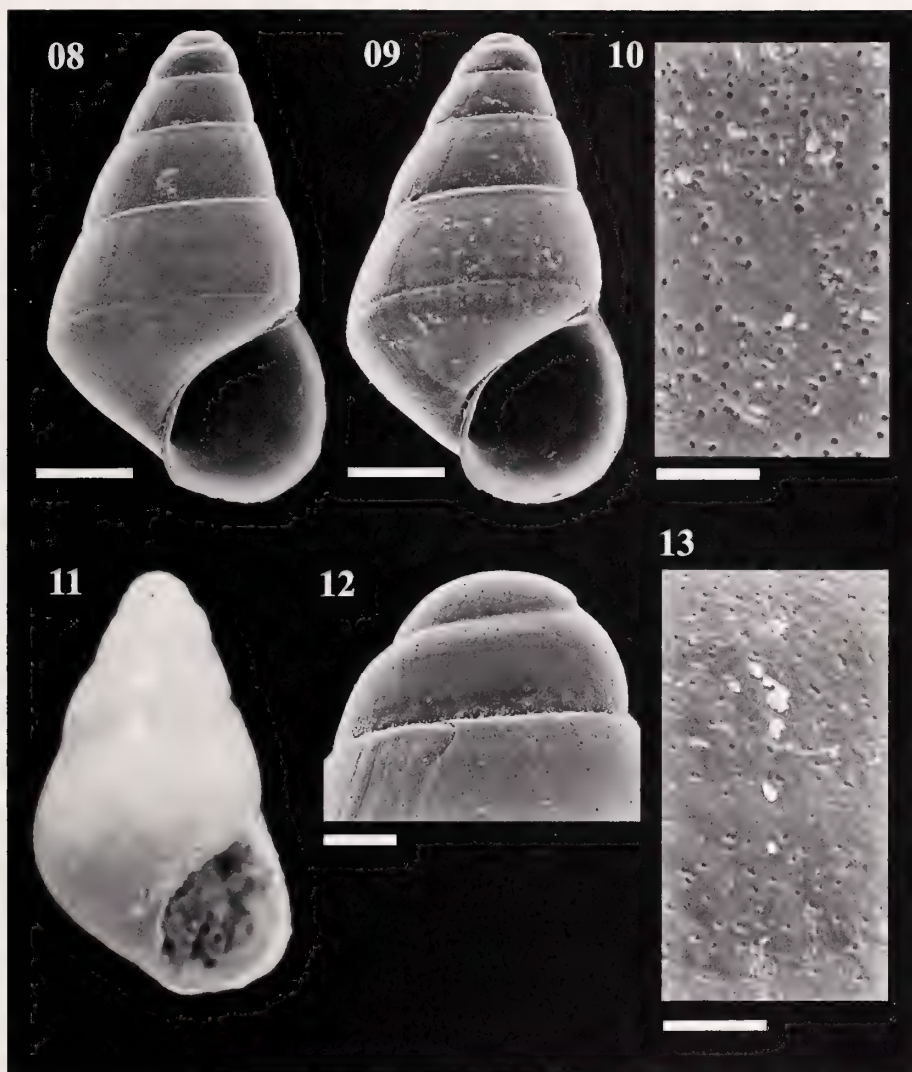
Etymology: *carinata* from Latin, *carina* referring to the spiral keels that ornament this species.

Range: Northeast Brazil.

Remarks: *Caelatura carinata* shares its prominent spiral sculpturing with all other species in this group (*C. spirocordata*; *C. tigrina* and *C. specularunda*; *C. phrix* n. sp. and *C. tupi* n. sp.). *Caelatura carinata* n. sp. is unique in that the protoconch is more hemispherical and smooth, whereas in the other species the beginning of the protoconchs are dome-shaped and show no clear boundary between the protoconch and teleoconch, with spiral ornamentation being continuous in both teleoconch and protoconch. Furthermore, in *C. carinata* n. sp. the whorls are strongly medially-angled, whereas all the others have convex whorl profiles.

***Caelatura noxia* n. sp. (Figures 20–22, 24–27)**

Description: Shell minute, elongate-pupoid, whorls convex, slightly staggered, cream to orange-reddish, lustrous, opaque. Protoconch paucispiral, 4–5 strong spiral rounded cords. Teleoconch with 4–5 strong undulating rounded spiral cords intercalating spiral



Figures 8–13. *Caelatura aulakion*. n. sp. 08. holotype (MNRJ 10308), length 2.2 mm; 09. paratype (IBUFRJ 14181), length 1.25 mm; 10. sculpture of the teleoconch of paratype; 11. *Caelatura rustica* syntype (BMNH 1887.2.9.1969–74), length 2.1 mm; 12. protoconch of holotype; 13. detail of the protoconch of paratype. Scale bar: 08–09: 400 μ m; 10–13: 10 μ m; 12: 100 μ m.

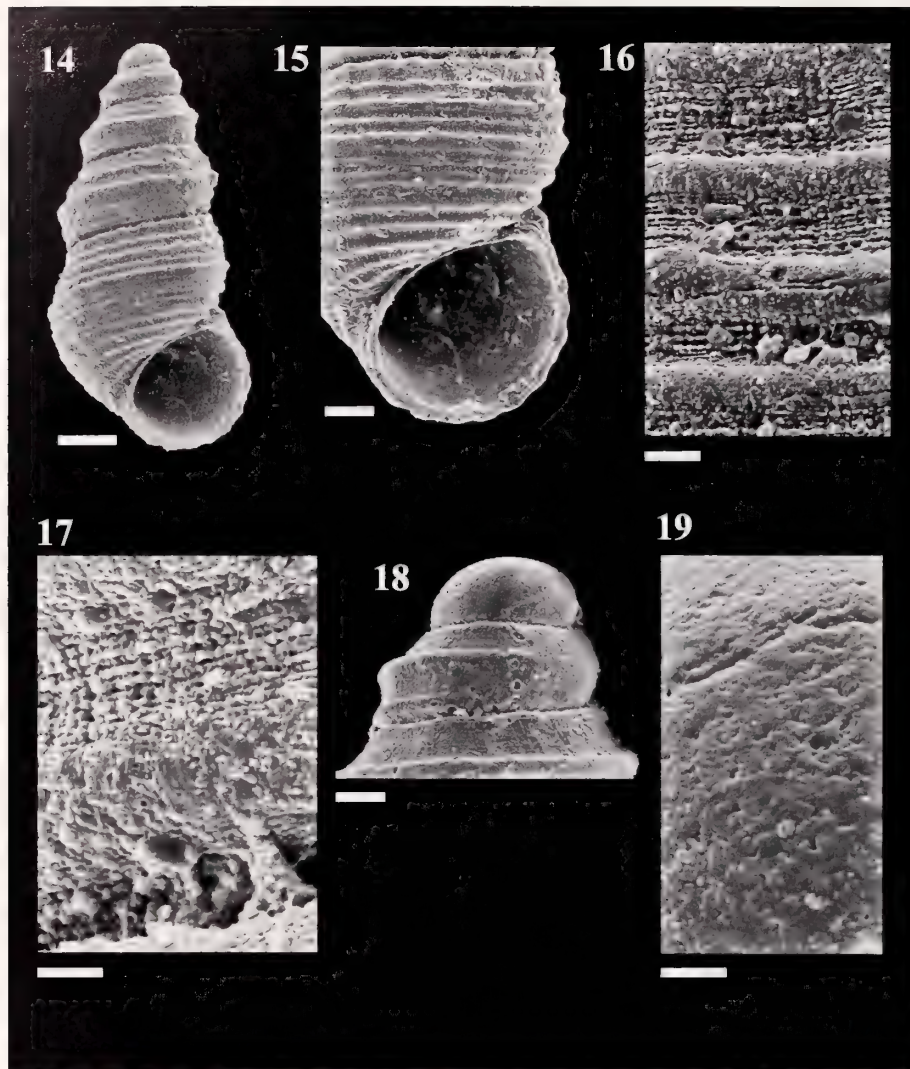
cordlets, cordlets about 1/3 of width of cords. Deep incised groove between cords, cordlets with same cord width, with additional very fine spiral sculpturing of about 10 laminate ridges. Numerous deep pits aligned over top of spiral cords. Suture impressed. Base convex with about 7 spiral cords. Aperture suboval, varicose. Minute chink-like umbilicus. Operculum oval, red, sulcus along inner (columellar) edge, strong longitudinal rib in middle of operculum. A peg rises from the most posterior part of the longitudinal rib extending beyond inner edge, but a laminar expansion linking it to the main body of operculum.

Dimensions: Holotype with 3.5 whorls in teleoconch; height 2.6 mm; width 1.2 mm.

Type locality: REVIZEE Program Score Central, sta. vv38, 22°00'24"S, 40°05'15"W, 100 m, 21/vii/2001.

Type material: Holotype: MNRJ 10311; paratypes (one in each lot): IBUFRJ 9520; DOUFPE 5026; MORG 41070; MZUSP 43202; MNHN; ZMA 4.04.044; IBUFRJ 14183. All from type locality.

Additional material: IBUFRJ 11941, sta. 20 raso, 19°16'05"S, 38°00'32"W, 67 m, 28/vi/2001, [1]; IBUFRJ 9800, sta. vv38 19°28'00"S, 38°22'00"W, 29/ii/1996 [115]; sta. 24 20°21'00"S, 36°38'00"W, 55 m, 13/vi/2001; IBUFRJ 8139, sta. D39, 19°28'00"S, 38°22'00"W, 74 m, 29/ii/1996, [1]; sta. C61, 20°30'38"S, 37°19'06"W, 24/iv/1996, [1]; IBUFRJ 10221, sta. C62, 20°30'02"S, 37°28'51"W, 96 m, 25/iv/1996, [17]; IBUFRJ 9520, sta.



Figures 14–19. *Caelatura carinata* n. sp. 14. holotype (MNRJ 10307) length 1.45 mm; 15. aperture; 16, 17. microsculpture of the teleoconch; 18. protoconch; 19. detail of the protoconch of holotype. Scale bar: 14: 250 μ m; 15, 20: 100 μ m; 16: 20 μ m; 17, 19: 10 μ m.

C62, 20°30'02"S, 37°28'51"W, 96 m, 25/iv/1996, [34]; IBUFRJ 14184, sta. C62, 20°30'02"S, 37°28'51"W, 96 m, 25/iv/1996, [1], all REVIZEE Score Central; IBUFRJ 7461, Espírito Santo State, 20 m, 1994, [12]. IBUFRJ 13794, Piúma, Espírito Santo, 1993; sta. D39, 19°28'00"S, 38°22'00"W, 29/ii/1996 [1].

Etymology: *noxia* from Latin, referring to fault, error; see Remarks.

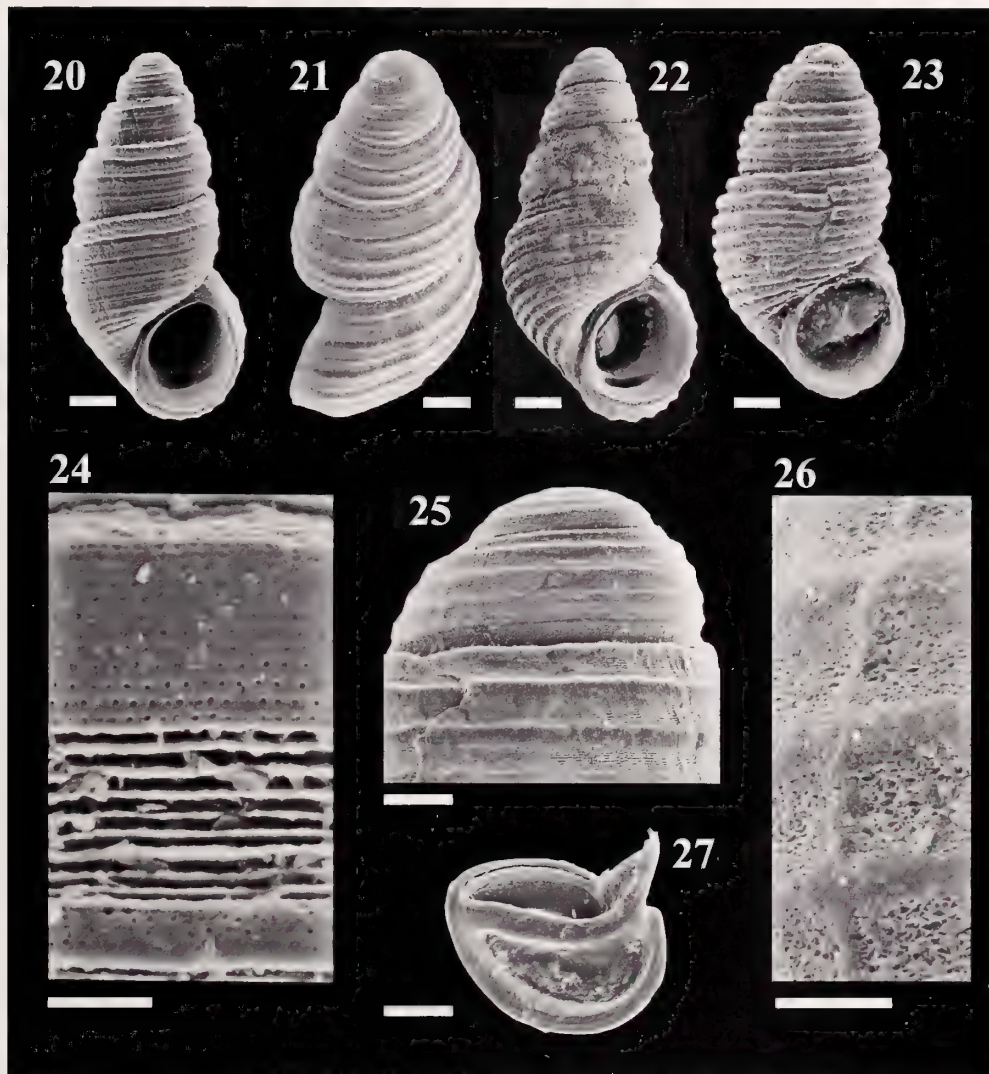
Range: Espírito Santo State, Southeast Brazil (19°16'05"S to 20°30'38"S).

Remarks: *Caelatura noxia* was erroneously illustrated as *C. spirocordata* by Absalão (2002: 3, fig. 9). However, *C. noxia* has more whorls in the teleoconch (4.5 in *C. noxia* 3.5 in *C. spirocordata*) and spiral

cords thinner than those of *C. spirocordata* (Figure 23), and also it has secondary spiral cordlets. The presence of secondary spiral cordlets and the length of shell effectively distinguish *C. noxia* from all other species.

***Caelatura phrix* n. sp.** (Figures 28–31, 33, 34)

Description: Shell conical-elongated, stout, opaque, first whorls slightly convex, body whorl broad. Protoconch paucispiral with 4 spiral cordlets. Teleoconch with 6 undulating rounded spiral cords, first two thinner and closer than others; third cord most prominent. Interspaces incised, broader than spiral cords and with about 18 somewhat irregular, corrugated bladed ridges. About 17 rows of deep pits on top



Figures 20–27. *Caelatura noxia* n. sp. 20. holotype (MNRJ 10311), frontal view, length 2.6 mm; 21. holotype showing varix (see arrow) behind aperture; 22. paratype (IBUFRJ 9520), length 2.02 mm; 23. *Caelatura spirocordata* (IBUFRJ 8505) length 1.7 mm; 24. detail of pits over top of the spiral cords at teleoconch; 25. protoconch of holotype; 26. detail of sculpture of the protoconch; 27. operculum of a spare specimen (IBUFRJ 14184). Scale bar: 20–23: 200 µm; 24, 26: 20 µm; 25: 50 µm; 27: 100 µm.

of spiral cords. Suture impressed. Base convex. Aperture rounded-oval. Outer lip varicose.

Dimensions: Holotype with 4.5 whorls in teleoconch; height: 2.7 mm; width 1.35 mm.

Type locality: REVIZEE Central V sta. 13B, 16°47'14"S, 38°41'14"W, 50 m, 30/vi/2001, RV "Astro Garoupa," Bahia State, northeast Brazil.

Type material: Holotype: MNRJ 10309; paratypes (one in each lot): IBUFRJ 11927; MORG 41073; MNHN; all paratypes from type-locality.

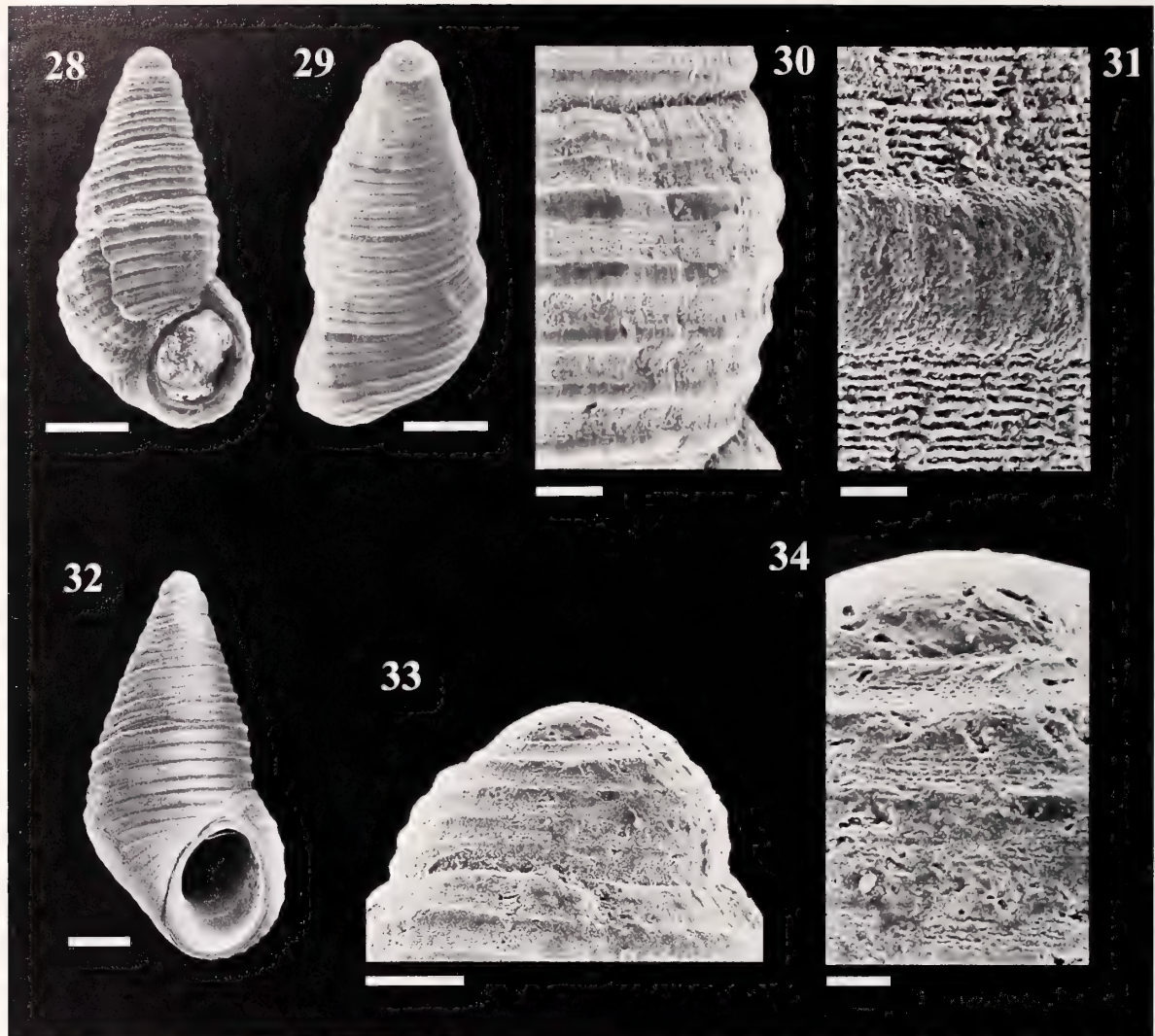
Etymology: *phrix* from Greek, referring to ripple, denoting the undulating axial ribs.

Range: Northeast of Brazil.

Remarks: *Caelatura phrix* n. sp. can be distinguished from all other spirally ornamented species of *Caelatura* by the presence of double minor spiral cords just below the suture. *Caelatura phrix* typically has conspicuous axial rounded ribs, but sometimes *C. tigrina* may have similar ornamentation. However, *C. tigrina* (Figure 32) has a more triangular spire profile and less convex whorls than *C. phrix* n. sp.

Caelatura tupi n. sp. (Figures 35–39)

Description: Shell conical, stout, whorls slightly convex, cream, opaque. Protoconch paucispiral, macroscopi-



Figures 28–34. *Caelatura phrix* n. sp. 28. holotype (MNRJ 10309), length 2.7 mm; 29. holotype showing varix; 30. sculpture of the teleoconch; 31. detail of microsculpture of the teleoconch; 32. *Caelatura tigrina* paratype IBUFRJ 12037; 33. protoconch of holotype; 34. detail of protoconch of holotype. Scale bar: 28, 29: 500 μ m; 30, 33: 100 μ m; 31, 34: 20 μ m; 32: 200 μ m.

cally smooth, with 3–4 spiral cords. Teleoconch with 5–6 undulating rounded spiral cords, sometimes intercalated with one spiral cordlet. Incised interspaces broader than spiral cords, showing about 9 corrugated spiral ridges. Top of spiral cords with about 12 rows of deep pits. Suture impressed. Base convex. Aperture oval. Outer lip thick. Inner lip thin. Minute umbilical fissure.

Dimensions: Holotype with 3.5 whorls in teleoconch; height 1.9 mm; width 1.0 mm.

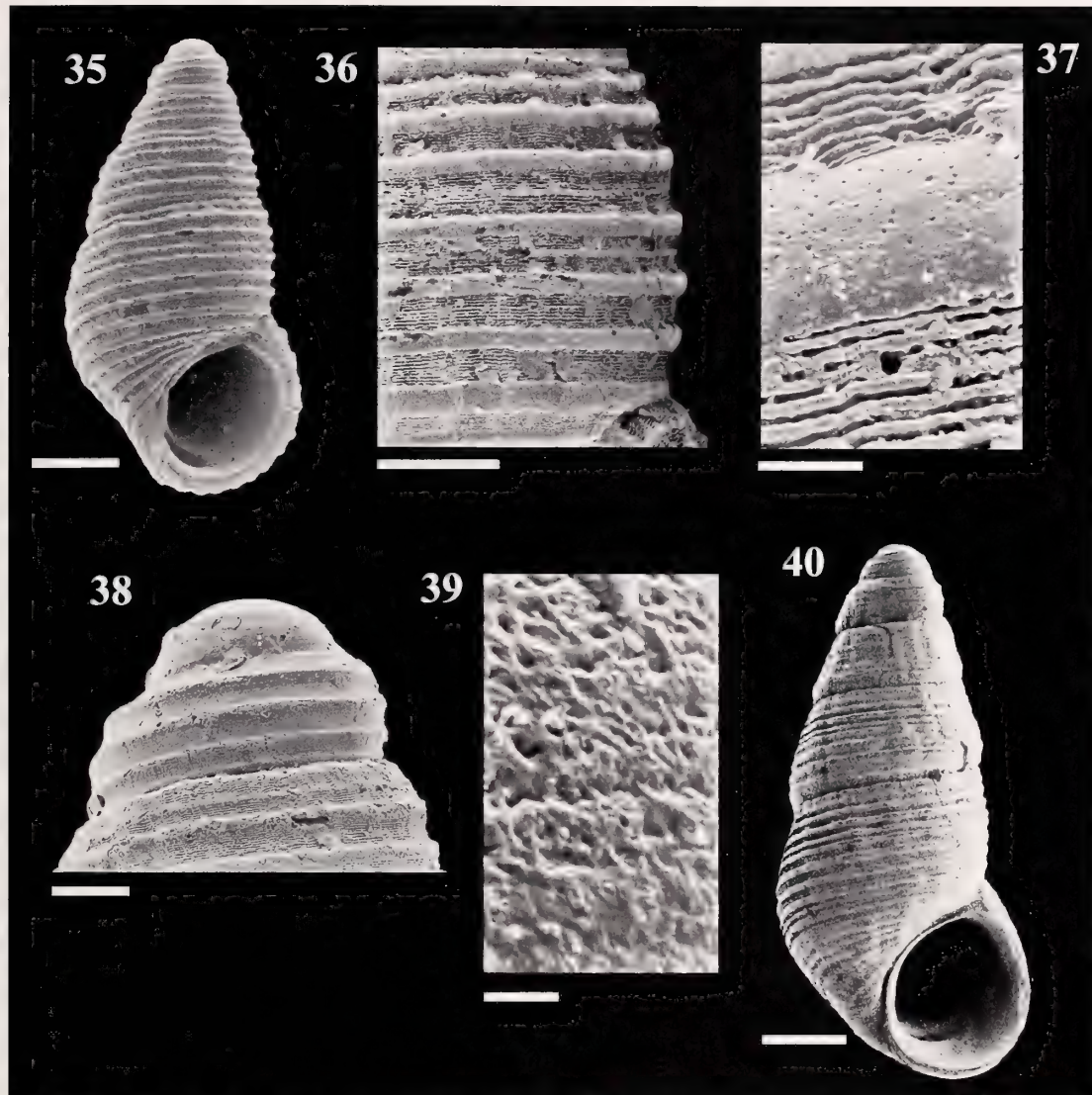
Type locality: REVIZEE V sta. 13B, 16°47'14"S, 38°41'14"W, 30/vi/2001, 40 m, RV "Astro Garoupa," Bahia State, Northeast of Brazil.

Type material: Holotype: MNRJ 10310; paratypes (one for each lot): IBUFRJ 14180; MZSP 43444; MORG 41074; ZMA 4.04.047; DOUFPE 5024. All paratypes from type-locality.

Etymology: *tupi* is the name of the one of the largest Indian tribes which inhabited Brazil in the sixteenth century; noun in apposition.

Range: Northeast Brazil.

Additional material: Revizee V sta. 20 19°16'05"S, 38°00'32"W, 67 m, 28/vi/2001; Revizee Central I sta. vv21 20°28'00"S, 40°00'00"W, 25.37 m, 26/ii/1996; Revizee V sta. 44 20°51'00"S, 33°38'00"W, 65 m, 11/



Figures 35–40. *Caelatura tupa* n. sp. 35. holotype (MNRJ 10310), length 1.9 mm; 36. sculpture of the teleoconch; 37. detail of microsculpture of the teleoconch; 38. protoconch of holotype; 39. detail of sculpture of the protoconch; 40. *Caelatura speculabunda* holotype (MNRJ 8621), length 2.46 mm. Scale bar: 35, 40: 400 μ m; 36: 10 μ m; 37: 200 μ m; 38: 100 μ m; 39: 5 μ m.

vii/2001; Bacia de Sergipe/Petrobras sta. 9.2 Am.2 11°30'08"S, 37°07'56"W, 900 m, 19/iv/2002.

Remarks: The regular spire profile and slightly convex form of *C. tupa* distinguish it from the almost flat whorls of *C. tigrina*, from the convexity in the posterior part of the whorls of *C. speculabunda*, from the more pupoid shell and thicker spiral cords of *C. spirocordata*, and from the more convex whorls of *C. noxia*.

Caelatura noxia n. sp. and *C. tupa* share the presence of secondary spiral cordlets between the main spiral cords, and distinct microtextures, visible only under high magnification. These two species can be separated by their overall shell profile, more triangular in *C. tupa*

and more pupoid in *C. noxia*. Furthermore, the secondary spiral cordlets are always present in *C. noxia*, whereas they are only sporadically present in *C. tupa*.

Discussion

Although not all of the species are sympatric, they all occur in the Caribbean Province (Palacio, 1982) and there is little morphological variation among populations within species. An exception is *C. barcellosi* which shows umbilicate and non umbilicate populations (see Absalão 1995: 89) but there is no evidence for geographic variation or subspecies. Besides that, we

know so little about the real distributional patterns of these minute molluscs that any attempt to establish biogeographical relationships would be too speculative.

The group formed by *C. albertoi*, *C. aulakion*, *C. rustica* and *C. gerhardtae* is characterized by its "smooth" appearance and it somewhat resembles some West African species described by Gofas (1995) as *Pseudodiala*. In a strict conchological sense, *Pseudodiala* could be distinguished from *Caelatura* based on punctures both on the protoconchs and teleoconchs, although this character seems quite variable and future anatomical studies should resolve this matter. On other hand, *C. carinata*, *C. noxia*, *C. phrix* and *C. tupi* share among themselves a characteristic ornamentation pattern of the spiral cords with broad interspaces between them displaying unusual blade like laminae ridges. Although definition for the genus *Caelatura* comprises smooth, spirally and/or axially ornamented shells, it is possible that future anatomical researches will prove that the usual *Caelatura* concept may be polyphyletic.

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Freshwater Mussel (Bivalvia: Unionidae) Causes Incidental Fish Mortality

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Abstract. A rare observation of incidental fish mortality caused by a native Atlantic slope freshwater mussel is herein reported from a small pond in Middleboro, Massachusetts, and the resulting mortality of the fish is discussed in the context of other vertebrate mortalities induced by aquatic invertebrates as reported in the literature.

On 14 August 2003, while surveying the south side of Tispaquin Pond (at the boat launch) in Middleboro (Plymouth Co.), Massachusetts, for specimens of the invasive Asiatic clam, *Corbicula fluminea* (Müller, 1774) (Bivalvia: Corbiculidae), a single living specimen of the eastern Elliptio mussel, *Elliptio complanata* (Lightfoot, 1786) (Bivalvia: Unionidae), was hand-collected in sandy substrate at one meter depth. Upon extracting the specimen for examination, a dead, juvenile yellow perch, *Perca flavescens* (Mitchill, 1814), about 5 cm long, was found lodged tightly between the valves (Figure 1). Both specimens were immediately retained, narcotized with Epsom salts, fixed in an ethyl alcohol series, preserved in 70% ethyl alcohol, and retained in the author's personal collection.

The yellow perch appeared to have died recently, as evidenced by the lack of glossing over its eyes and the relatively good condition of scales and fins. No evidence of decomposition was evident whatsoever. Cause of death appeared to be from the trauma caused by the mussel valve closure around the body of the fish. The eastern Elliptio was 8.3 cm long with valves clamped tightly around the body of the fish at right angles to the midline and directly through the region of the dorsal fin. The mussel valves remained clamped throughout the fixation and preservation process and the fully preserved fish continues to remain clamped between the valves of the preserved mussel at the time of submittal of this manuscript (October 2006). The mussel did not appear adversely affected by the presence of the yellow perch, although the valves could not close completely and remained agape even after retrieval from the substrate. Although numerous (hundreds) other specimens were collected from the site at that time and subsequently, no other specimens have ever been found with valves clamped around juvenile fishes.

Incidents of mortality in fish and other aquatic vertebrates are commonly attributed to predation by other vertebrates. Vertebrate mortality caused by

invertebrates, especially upon adult aquatic vertebrates, is extremely rare. Predation of hatchling or juvenile reptiles, particularly turtles, is known for decapod crustaceans (Stancyk, 1982) and hemipterans (Gotte, 1992). Active predation by aquatic invertebrates is known for diving beetles (*Dytiscus* sp.) and dragonfly nymphs (*Anax* sp., and others) on various amphibians (e.g., salamanders, tadpoles) (Smith & Van Buskirk, 1995; Storfer & White, 2004; Van Buskirk & Schmidt, 2000). Recently, Mueller et al. (2006) documented significant predation on eggs and larvae of the endangered razorback sucker, *Xybauchen texanus* (Abbott, 1860), by the introduced red swamp crayfish, *Procambarus clarkii* (Girard, 1852). Back in 1894, J.H. Sage (1895: 49, unnumbered fig.) published a short observation near Portland, Connecticut, of a living sora, *Porzana carolina* (Linnaeus, 1758), with a living adult freshwater mussel (later identified as *Elliptio complanata*) clamped tightly to its left foot. The bird was unable to fly and was hopping about with its toe nearly severed. Frierson (1899: 139–140) reported twice killing ducks with freshwater mussels attached to their toes and postulated this as a means of long-distance dispersal. Carbine (1942) documented attachment of the fingernail clam, *Musculium securis* (Prime, 1852), to the jaws of two live individuals of northern pike, *Esox lucius* Linnaeus, 1758, in Houghton Lake, Michigan. DeGroot (1927) reports the introduced ribbed mussel, *Geukensia demissa* (Dillwyn, 1817) (Bivalvia: Mytilidae), trapping its valves onto the toes and beaks of foraging clapper rails, *Rallus longirostris* Boddaert, 1783, in San Francisco Bay, California. In addition to personally removing a mussel from a nesting chick's toe, the author estimated 75% of the rails in the region had lost one or more toes to ribbed mussels and inferred frequent mortality, especially for rail chicks. Plummer and Goy (1997: 88, fig. 1) documented, in graphic detail, a living adult pondmussel, *Ligumia subrostrata* (Say, 1831), causing mortality of a common musk turtle, *Sternotherus odoratus* (Latrielle, 1802), in



Figure 1. Yellow perch (*Perca flavescens*) (5.0 cm) trapped within eastern Elliptio (*Elliptio complanata*) (8.3 cm).

a similar fashion in Salado Creek, near Floral (Independence Co.), Arkansas, in 1996. The mussel was found to be a 73.2 mm gravid adult female that had apparently closed its valves upon the turtle's neck just ventral to the siphons laterally compressing it to 2.4 mm causing mortality either by drowning or suffocation.

Freshwater mussels are known to feed on a variety of particles including bacteria, protozoans, and phytoplankton (Coker et al., 1921; Gatenby et al., 1996; Nichols & Garling, 2000; Paterson, 1986; Yeager et al., 1994). Active feeding by mussels on fish, hosts or otherwise, has never been documented, however, nor is it implied here.

Mantle displays by various species of freshwater mussels have been shown to elicit attacks by various fish resulting in gill and body infestations of the fish by mussel glochidia (Haag & Warren, 1999; Kat, 1984), but have not been demonstrated for eastern *Elliptio* despite extensive morphological study of this species (Downing et al., 1993; Kesler & Bailey, 1993; Matteson, 1948, 1955; Watters et al., 2005; Weir, 1977; Wiles, 1975a, b; Young, 1911). Yellow perch is a confirmed glochidial host for eastern *Elliptio* along

with seven other common freshwater fish species (Lefevre & Curtis, 1912; Matteson, 1948, 1955; Tedla & Fernando, 1969; Weir, 1977), nearly all of which are present in Massachusetts waters (Hartel et al., 2002). The collected specimen was not found to be gravid and no encysted glochidia were found on the trapped fish. Although speculative, it is unlikely the trapped yellow perch was attracted to any sort of display behavior.

The combination of wide habitat preference, large scale distribution, high densities, and glochidial transformation capability on multiple, common fish hosts indicates *Elliptio complanata* is an ecological generalist. The mortality of the yellow perch in this case may have been incidental. Although speculative, it is not likely the mussel was attempting to feed on the fish nor luring the fish in order to infect it with glochidia. The mussel may have been filtering with its valves agape and the fish somehow managed to find itself in the wrong place at the wrong time. A paucity of similar observations in the literature despite numerous, long-term studies of freshwater mussels in the past century indicates the observation presented here is a randomized, rare event that is not part of the typical life history of freshwater mussels.

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Fallacies Underlying the Assumption of Calcium Limitation on the Evolution of Land Snails in Bermuda

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Abstract. The supposed lack of calcium during glacial periods of red soil development has been cited as the principal factor influencing evolution in land snail shells on Bermuda during the Quaternary. We argue that at no time was there an appreciable deficiency of calcium carbonate on Bermuda because the red soils themselves are largely made up of carbonate and because calcium in plant tissues would have been recycled during all stages of the Quaternary by frequent forest fires. Supposed instances of very localized changes in shell thickness arose through misinterpretation of chronology. Paedomorphic populations of the subgenus *Poecilozonites* occur only in carbonates of the last interglacial (Marine Isotope Stage 5) and the Holocene, never in glacial red soils as maintained repeatedly by Gould.

INTRODUCTION

In several studies, Gould (1966, 1968, 1969, 1970a, b, 1971a, b) investigated evolutionary trends in diversity of shell size and shape in land snails, particularly of the genus *Poecilozonites*, subgenus *Poecilozonites* (Zonitidae), on the remote, oceanic island of Bermuda. He repeatedly hypothesized that the lack of calcium carbonate during glacial episodes, when snails were supposedly living on lime-poor red soils, was of prime importance in driving evolution in Bermudan snails.

In attempting to explain repeated instances of paedomorphosis in the subgenus *Poecilozonites*, Gould (1968: 81) stated that: “The most paedomorphic subspecies originated in red soils; paedomorphs did not evolve in times of carbonate-dune deposition. The thin shells of paedomorphs might have been adaptive in the low-calcium environment of red soils.” Gould (1977: 277) later unequivocally identified the “adaptive trigger” of paedomorphosis as “the almost totally lime-free soils that served as substrate for the most paedomorphic forms.”

Calcium-poor red soils supposedly not only explained paedomorphosis but also influenced evolution in other lineages in the subgenus (Gould, 1969: 482–492). For example, in the giant species *P. nelsoni* “a thin-shelled subspecies lived in red soils” (Gould, 1969: 491).

In another study, Gould (1970a: 572) proposed that variations in relative abundance or shell morphology in six different species or populations of land snails on

Bermuda during the last two glacial cycles “was influenced primarily by the availability of calcium carbonate for shell construction.”

And in yet another case (Gould, 1971a: 91), what were interpreted as very restricted local populations of several different snails were thought to differ from their supposed contemporaries elsewhere in the island because of local soil conditions, thus providing support for Gould’s “previous assertion (Gould, 1968 and [1969], pp. 482–483) that the adaptive significance of paedomorphosis ... lies in the thin shell that it produces and that lime-poor habitats require.”

A much more refined knowledge of the stratigraphy and geochronology of Bermuda (e.g., Vacher et al., 1989, 1995; Hearty, 2002; Hearty et al., 2004) than was available to Gould presents a very different picture of the evolution of the island’s snails. The progress achieved in unraveling the complex limestone architecture of Bermuda’s sedimentary units and their ages can be partially attributed to traditional and new applications of amino acid racemization (AAR) geochronology (Hearty et al., 1992). We have determined the degree of epimerization of D-alloisoleucine/L-isoleucine (or A/I) from several populations of *Poecilozonites* including *P. bermudensis bermudensis*, *P. b. fasolti*, and other paedomorphs (Tables 1 and 2). AAR geochronology provides an independent means with which to determine relative ages and age-succession of the land snails in question. A/I is determined on several individual snails from each sample. A/I values are approximately 0.015 in living specimens, 0.40 to 0.58

Table 1

Taxa of *Poecilozonites* (*Poecilozonites*) discussed in this paper with their old and revised chronologies. Each of the main lineages (*P. b. bermudensis*, *P. b. zonatus*, and *P. nelsoni*) was considered by Gould (1969) to be continuous across their age ranges. The stratigraphic names used in Gould (1969) are poorly defined in terms of both stratigraphic position and apparent age (see Hearty, 2002). We offer only inferences of what Gould may have meant by use of these stratigraphic names.

Taxon	Old chronology (ages inferred from Gould, 1969)*	Revised chronology (estimated age ka) This study	Correlated marine isotope stage (MIS)	Comments
<i>P. b. bermudensis</i> (Pfeiffer, 1845)	St. Georges, Southampton, Recent (80 ka to present?)	Holocene (12 ka -present)	MIS 1 only	The modern phyletic lineage evolved independently of paedomorphs in the Pleistocene.
<i>P. b. zonatus</i> (Verrill, 1902)	Shore Hills (>300 ka?) to St. Georges (80–10 ka?)	Interglacial intra-dune and post highstand soils (130–80 ka)	All MIS 5 only	Considered to be the trunk species of all <i>P. bermudensis</i>
<i>P. b. fasolti</i> (Gould, 1969)	Shore Hills (>300 ka?)	Holocene cave colluvium (1–2 ka)	Late MIS 1	Differs only slightly from other late Holocene morphotypes
<i>P. b. siegmundi</i> (Site 6; Ireland Isl.) (Gould, 1969)	Harrington red soil (post 125 ka?)	Interglacial intra-dune soils (c. 100–115 ka)	Mid MIS 5	AAR ratios indicate <i>P. b. siegmundi</i> and <i>P. b. sieglindae</i> are the same mid MIS 5 age
<i>P. b. sieglindae</i> (Site 5; Rocky Bay) (Gould, 1969)	Pembroke and Harrington red soil (post 125 ka?)	Interglacial intra-dune soils (c. 100–115 ka)	Mid MIS 5	Two additional unnamed last interglacial age paedomorphs are of similar (St. Georges), or slightly older ages (Hamilton) compared to the named subspecies
<i>P. nelsoni</i> (Bland, 1875)	Shore Hills (>300 ka?) to St. Georges (80–10 ka?)	Glacial red soils (180–130 ka and 80–10 ka)	MIS 6, 4–2	Nearly identical <i>P. nelsoni</i> morphotypes are found in three successive glacial-age soils

from shells from Marine Isotope Stage (MIS) 5 (last interglacial), and progress to an equilibrium ratio of 1.30 after perhaps 1,000,000 yr (Hearty et al., 1992). With independent ^{14}C or U/Th age calibration at key intervals in the epimerization reaction, it is possible to compute absolute age estimates directly from A/I. Relevant discussion and protocols regarding this application and underlying database are available in Hearty et al. (2004).

Before detailing evolutionary sequences and the possible causes in subsequent papers, we wish to dispose of the fallacious assumptions and erroneous facts associated with the hypothesis of the effects of carbonate limitation on the evolution of Bermudan snails. It is highly unlikely that any significant area of Bermuda was deficient in calcium at any period during the entire post-volcanic history of the island. In one lineage, snails during glacial periods deposited far more calcium in their shells than during interglacial times. Gould's (1971a) instance of highly local environmental control was based on an erroneous assumption of the

age of the sample. And finally, in complete contrast to Gould's repeated assertions, all of his fossil examples of paedomorphs existed during interglacial times of high carbonate deposition and never occur in glacial red soils.

AVAILABILITY OF CALCIUM ON BERMUDA

To begin with, Gould's correlation of shell variation with the amount of calcium carbonate in the substrate is compromised by Goodfriend's (1986) detailed review of causes of variation in shells of land snails. Gould (1968) cited investigations by Rensch (1932) and Oldham (1934) as showing calcium deprivation to result in shell thinning or mortality in snails. Yet the same papers are cited by Goodfriend (1986: 208) as finding ambiguous results for a correlation between shell size and limestone availability. Goodfriend (1986: 208) concluded that field studies "failed to reveal any relationship between shell size and the calcium-

Table 2

Amino acid ratios on *Poecilozonites b. bermudensis* (Pbb), *P. b. fasolti* (Pbfas), *P. b. sieglindae* (Pbsl), *P. b. siegmundi* (Pbsm) and unnamed paedomorphs (paed) from Bermuda. Gould (1969) collections from the MCZ are identified by "SJG" prefix. Our collections from numbered Gould (1969) sites are preceded by our field number, then Gould's. NAU-AAL = sample number from Northern Arizona University Amino Acid Laboratory. Age interpretations not in years refer to Marine Isotope Stage (1 = Holocene; 5 = last interglacial). Gould's Tom Moore's Cave is thought to be the same as either Walsingham Cave or Walsingham Sink Cave. The date for Fern Sink Cave is based on a charcoal AMS ^{14}C age of 1630 ± 60 yr BP (Hearty et al., 2004).

Site # Fig. 1	FMNH	NAU-AAL	FIELD #	Spp	Locality information	Age/Interp.	Mean	St Dev	N=
—	—	4081	ANSP 85510	Pbb	Alive 1903	104 yr	0.017	0.001	1
2	303192-3	3841	SJG53	Pbfas	Tom Moore's Cave <i>P. b. fasolti</i> (Gould's collection)	Late 1	0.055	0.034	2
2	303194-5	3847	UGC1z(2a)	Pbb	Fern Sink Cave upper	1,630 yr BP	0.047	0.014	3
2	303196	4575-77	UWV1	Pbb	Walsingham Cave	Late 1	0.045	0.017	3
2	303197	4578-80	UWS1	Pbb	Walsingham Sink Cave, entrance	Late 1	0.046	0.019	3
2	303198	4403, 05	UWSu2	Pbb	Walsingham Sink Cave, deeper deposit	Late 1	0.069	0.008	2
2	303199	3845	UGC1x(2)	Pbb	Fern Sink Cave lower level	Mid 1	0.097	0.023	3
7	303200-1	4607-10	UTB1/2	Paed	Tobacco Bay, St. Georges	Late 5	0.40	0.03	3
5	303202-4	790514.1	URB-SJG 44	Pbsl	Rocky Bay, type <i>P. b. sieglindae</i>	Mid 5	0.51	0.01	2
6	303205-8	3838-29	UIII-SJG10	Pbsm	Ireland Island, type <i>P. b. siegmundi</i>	Late 5e	0.523	0.027	6
8	303209	3837	USL1d	Paed	Shell Depot	Late 5e	0.542	0.05	3
9	303210	3864	USS1c	Paed	Saltus School, 1989	Mid 5e	0.587	0.021	3

carbonate content of the substrate" and that "experimental studies give similarly inconsistent results."

But it is one thing to suggest that lime-poor soils drive snail evolution and another to show that snails on Bermuda ever experienced lime-poor soils. The island of Bermuda (Figure 1) is composed almost entirely (over 95% of surface rocks) of lithified dunes of calcium carbonate sand formed from skeletal remains of marine invertebrates and coralline algae. Dune deposition takes place during interglacial periods when sea levels are elevated (Bretz, 1960). During the depressed sea levels of glacial periods, when the entire

Bermuda platform is exposed, marine carbonate supply is cut off and red soils form from diagenesis of limestone and from wind-borne dust (Bricker & Mackenzie, 1970; Muhs et al., 1990), which is more abundant in the atmosphere and polar ice during glacial periods (Glacuum & Prospero, 1980).

Because they are developed directly on limestone, most soils on Bermuda contain large amounts of calcium carbonate (CaCO_3), often in the form of carbonate sand or silt. Of the 45 samples in 9 soil profiles analyzed by Ruhe et al. (1961: their tables 3, 4), 41 were more than 80% CaCO_3 , and only 4 were below 14.6% (all from subsurface horizons in the more ancient soils). The upper and surface samples in each profile were all above 63% CaCO_3 . All levels in the deep deposits of Admirals Cave, which span the past 120 kya and thus include both glacial and interglacial slope wash sediments, contain at least 70% CaCO_3 (Hearty et al., 2004).

The thickest soil development on Bermuda occurred during a prolonged period of depressed sea-levels from about 800 kya to 450 kya—the Big Red Soil of Hearty et al. (2004) and Olson et al. (2005). No specimens of land snails are known from this period and all of those studied by Gould are younger. Regardless, it is unlikely that snails in Bermuda ever lived on soils that were substantially lacking in calcium.

Even during glacial periods when red soils develop, areas of high relief and any erosional features would expose bare carbonates, particles of which would be carried by wind or water to places where carbonates are

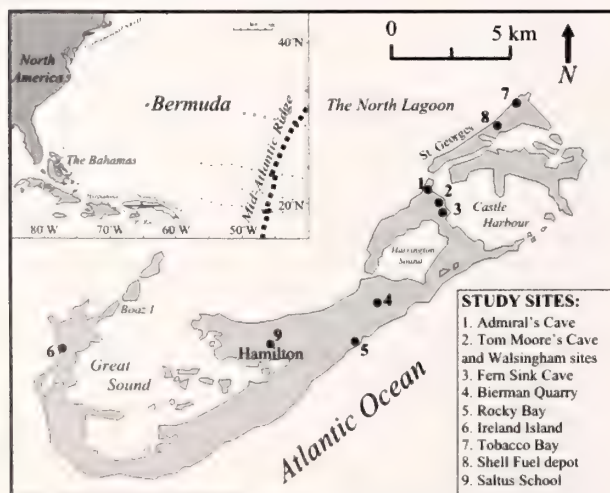


Figure 1. Location map of sites discussed in the text.

covered by soil. Furthermore, snails need not derive calcium directly from the substrate, as they would also obtain substantial amounts of calcium from plant detritus. Calcium is necessary for the formation of plant cell walls, where once incorporated it remains inert. Thus it is necessary for new growth, so that plants themselves would not thrive on truly calcium deficient soils. If there actually were local areas where soils were deficient in calcium, these would nevertheless receive calcium from plant detritus blowing from areas higher in CaCO_3 and from CaCO_3 dust from the shore and erosional features exposing limestone.

The roots of larger plants on Bermuda such as palmetto (*Sabal bermudiana*) and particularly cedar (*Juniperus bermudiana*) would be able to penetrate soils to take up calcium directly from underlying carbonate deposits. Calcium sequestered in plant tissues such as dead leaves, bark, and wood, would be released in ash after burning. Bermuda experienced numerous natural fires probably throughout its history. We found charcoal, sometimes in great quantity, throughout the entire sequence in Admirals Cave (location in Figure 1) representing the last 120 ky of Bermuda's history (Hearty et al., 2004). We have also seen evidence of extensive natural burning in glacial soils of MIS 10 (about 300 ± 30 ky old) exposed in Bierman's Quarry (location in Figure 1; see Olson et al. 2005 for information on this site). Thus, there were fires capable of releasing calcium stored in plant tissues throughout the entire the fossil record that Gould studied. In short, it is difficult to imagine any situation in which a Bermudan snail would be stressed to obtain sufficient calcium for shell building.

TOTAL SHELL CARBONATE IN GLACIAL VERSUS INTERGLACIAL SNAILS

It was Gould's (1969: 487) contention that "snails from red soils (glacial periods) tend to reach larger maximal sizes, have thinner shells and be smaller at a whorl than samples from eolianites." Shell thinning was supposed to be an indication of decreased calcium resources. But in none of his writings on the subject did Gould provide any quantitative measures of shell thickness or mass of Bermudan snails.

If calcium carbonate were ever a limiting factor in snail evolution in Bermuda we would expect this to be reflected in the total shell mass, regardless of thickness. From our excavations in the finely stratified deposits in Admirals Cave and from dating of specimens from many other sites around the island, we can now be quite confident about the sequence of shell forms in the subgenus *Poecilozonites* since the penultimate glaciation (Hearty et al., 2004). The last two glacial periods are characterized by the presence of the giant form known as *P. nelsoni*. Although this form evolved

independently in each of these glacial episodes, the forms are identical in size and shape so far as we have been able to determine. During the last interglacial, the widespread and abundant *P. b. zonatus* prevailed, and *P. b. bermudensis* characterized the present, Holocene, interglacial, although it is now perhaps extinct (Bieler & Slapcinsky, 2000). A sample of 10 shells of *P. nelsoni* had a mass of 37.7 g, whereas 10 shells of *P. b. zonatus* weighed 10.2 g, and 10 shells of fully mature individuals of *P. b. bermudensis* weighed 7.4 g, whereas 10 from a lot of smaller shells weighed 5.0 g. Although these are pretty simple statistics, additional data are not going to alter the fact that in this lineage of *Poecilozonites* individual snails were depositing 4 to 5 times as much calcium in their shells during glacial periods as their successors did during interglacials. This does not support Gould's idea of a deficiency of calcium carbonate during glacial periods.

A CASE OF "UNUSUAL PRECISION" OF ENVIRONMENTAL CONTROL NEGATED

Gould (1971a) cited a sample containing five species of snails from what he believed to be a Pleistocene red soil deposit (his "Shore Hills Soil") at a site that he called Tom Moore's Cave as being an example of an "extremely local event" in which very tight environmental control was exerted on shell morphology. In all five species the umbilical widths were greater than in "contemporaneous" samples from elsewhere on the island, meaning those that were also believed to be derived from the Shore Hills Soil.

The large umbilicus was said to be negatively correlated with shell thickness (i.e., shells were thinner), which in turn was believed to be a response to low CaCO_3 levels in the soil. Thus, supposedly, over a small area of lime-deprived soil, all five species developed thin shells and large umbilici, whereas their supposedly contemporaneous nearby neighbors with greater availability of lime did not. What Gould did not mention, however, is that the snails from Tom Moore's Cave are also exactly like the modern representatives of the same species.

The greatest error to which Gould was subject in his studies of Bermudan snails was his belief that all samples from caves and fissures, which were associated with red soils, came from what he regarded as a middle Pleistocene Shore Hills Soil (Sayles, 1931) and were broadly contemporaneous. We now know, however, that snails and their enclosing soils in fissures and caves are not all contemporaneous. This is explained by the sedimentary process of fissure and cave filling. As a "pitfall" void opens to the surface, the capping soils on the host limestone, which may be hundreds of thousands of years old depending on the formation, would fill the void. In addition, organisms living at the

Table 3

Simple morphometric data from Bermuda *Poecilozonites* paedomorphs discussed in this study. Rows in **bold** are from Gould's MCZ collections, and in plain type from our (O&H) field collections of Gould's and other relevant sites. Morphometric measures of Gould's (1969) *P. b. fasolti* (SJG53) and our sites from Walsingham Cave (UWV1) and Walsingham Sink Cave (UWS1) show no significant differences. With the exception of UGC1x, *P. b. fasolti* and our samples are statistically identical in size and shape. On the basis of morphometric and amino acid data, we are confident that we are dealing with the same populations as described in Gould (1969) and that *P. b. fasolti* is late Holocene and the same as *P. b. bermudensis*.

Gould (1969) samples our collections (O&H)	Shell width (mm)	$\pm 1\sigma$	Shell height (mm)	$\pm 1\sigma$	Height/Width	$\pm 1\sigma$	Total size (w + h, mm)	$\pm 1\sigma$	N
SJG53 <i>P. b. fasolti</i>	21.76	1.26	8.51	0.38	0.40	0.02	30.26	1.56	5
(O&H) <i>P. b. fasolti</i>	21.82	1.26	8.53	0.62	0.39	0.02	30.35	1.78	40
(O&H) UWV1 <i>Pbb</i>	21.86	0.81	8.60	0.66	0.39	0.03	30.46	1.28	15
(O&H) UWS1 <i>Pbb</i>	21.91	1.73	8.49	1.08	0.39	0.03	30.41	2.71	15
(O&H) UGC1z (1) <i>Pbb</i>	21.76	2.43	8.76	1.62	0.40	0.03	30.51	4.00	7
(O&H) UGC1x (2) <i>Pbb</i>	19.15	1.40	7.43	0.87	0.39	0.02	26.58	2.20	6
<i>P. b. bermudensis</i>	20.05	5.44	7.40	1.27	0.37	0.04	27.45	6.72	2
(O&H) Holocene <i>Pbb</i>	19.33	1.67	7.30	2.09	0.40	0.03	27.04	1.84	175
(O&H) Pleistocene " <i>Pbb</i> "	19.52	1.28	7.68	0.62	0.39	0.02	27.19	1.82	30
All paedomorphs	22.03	0.81	8.13	0.40	0.37	0.02	30.17	0.85	3
<i>P. b. siegmundi</i> (<i>Pbsm</i>)	21.90		8.50		0.39		30.40		1
(O&H) <i>Pbsm</i>	21.40	1.03	9.67	0.60	0.45	0.02	31.07	1.46	6
(O&H) <i>Pbsm</i>	20.93	2.57	8.53	2.03	0.40	0.05	29.47	4.60	3
<i>P. b. sieglindae</i> (<i>Pbsl</i>)	21.30		7.70		0.36		29.00		1
(O&H) <i>Pbsl</i>	21.80		7.60		0.35		29.40		1

surface that succumb to the same pitfall would also be mixed with the ancient soils. This diachrony, explained in Hearty et al. (2004), was clearly not understood by Gould, leading to grave misinterpretation of the biostratigraphic succession of *Poecilozonites*. Snails that Gould assumed were from his Shore Hills Soil, which he thought to be between 0.3 to 1 million yr old (MIS 9 to ~25), include specimens from the last two glacial episodes (MIS 6 and 4/2), the intervening interglacial (MIS 5), and the Holocene (MIS 1) (Hearty et al., 2004).

We have not been able to determine with absolute certainty which of several caves near Tom Moore's Tavern is the one from which Gould obtained his sample, but from our reconnaissance of the area it is most likely that this cave was one of two now known as Walsingham Cave and Walsingham Sink Cave (Olson et al., 2005), probably the latter. In Walsingham Cave the fossils in sediments that we found were entirely Holocene in age. In Walsingham Sink Cave, both in a rockshelter at the entrance and in a more extensive deposit deep in the cave, a thin veneer of loose Holocene sediments (by the inclusion of *P. b. bermudensis*) rested unconformably on a deeper, more compacted soil deposited during the last (Wisconsinan – MIS 2–4) glacial stage, as determined from the inclusion of *P. nelsoni* and the flightless rail *Rallus recessus* (Olson & Wingate, 2001; Hearty et al., 2004; Olson et al., 2005).

Regardless of the precise identity of Gould's Tom Moore's Cave, we have measured and analyzed a sample of Gould's *P. bermudensis fasolti* from his own collection (SJG site #53; Gould, 1969: p. 507) at the MCZ (Tables 2 and 3). Two shells of *P. b. fasolti* yielded a mean AAR ratio of 0.055 ± 0.034 . Although we have no independent ^{14}C ages for these specimens, a single *P. b. bermudensis* shell from nearby Fern Sink Cave (UGC1z) produced a mean ratio of 0.047 ± 0.014 (3) with an AMS ^{14}C age of $1,630 \pm 30$ yr BP (Table 2). The estimated age of Gould's sample of *P. b. fasolti*, based on the age of the Fern Sink sample (Hearty et al., 2004; and Figure 2), is 1900 ± 1200 yr. The late Holocene age of the Tom Moore's Cave sample is unquestionable; the larger error being the result of the limited number of shells analyzed. Additional samples from Walsingham Cave (UWV1) and Walsingham Sink (UWS1) caves gave similar mean A/I values and morphometry (Tables 2 and 3). At this very rapid early stage of the epimerization reaction, small differences in age (i.e., several hundred years) would result in significantly different A/I ratios. Because the method is destructive we chose to limit the number of shells damaged by sample extraction.

To summarize, the sample of snails that Gould (1971a) attempted to use to show "unusual precision" of environmental control in the middle Pleistocene is actually late Holocene in age, only 2 ± 1 ky old, and is

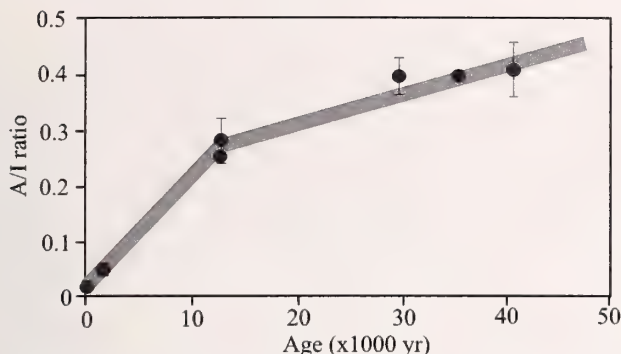


Figure 2. Accelerator mass spectrometry (AMS) ^{14}C calibration of *Poecilozonites* epimerization history over the past 40 ka (Hearty et al., 2004). All samples older than 10 ka are *P. nelsoni*, which has demonstrated a slightly faster ($1.2\times$) epimerization rate than *P. bermudensis*, or *P. b. zonatus*.

thus essentially modern in all respects. It tells us no more about evolution than any other modern sample.

THE SOILS ON WHICH PAEDOMORPHS ORIGINATED

Gould (1969) interpreted several populations of *P. bermudensis*, including the modern nominate subspecies, as paedomorphic offshoots that evolved independently at least 4 different times from non-paedomorphic stock. We agree with some aspects of this interpretation, namely that the forms are paedomorphs and that they evolved independently more than once. We will deal with the evolution of paedomorphs in another paper but here intend to take a closer look at Gould's extraordinary statement that the paedomorphs "originated in red soils; paedomorphs did not evolve in times of carbonate-dune deposition" (Gould, 1968: 81).

The modern taxon *Poecilozonites bermudensis bermudensis* was Gould's prime example of a paedomorph. This form occurred throughout the island in historic times, although it was apparently extirpated in the 20th century by introduced predators and other human-induced environmental factors. We now know that *P. b. bermudensis* evolved very rapidly at the beginning of the Holocene (Hearty et al., 2004), so it never existed in a glacial environment, or during a glacial episode. The Holocene is an interglacial episode with high concentrations of carbonates at the surface, although few of these surface carbonates are of Holocene age.

Gould (1969: 480, fig. 20) thought that his *P. b. fasolti* was the earliest of the various paedomorphic offshoots, supposedly originating in the red middle Pleistocene "Shore Hills Soil." As discussed above, however, topotypical paratypes of *P. b. fasolti* (SJG #53) are only 2 ± 1 ky old, hence essentially modern. Thus *P. b. fasolti* becomes a synonym of *P. b.*

bermudensis and is not associated with a glacial period or glacial soils.

We collected new material from most of the other sites in which Gould identified paedomorphs as well as in several additional sites that we discovered. We determined A/I ratios from this new material and also from Gould's original material stored at MCZ. As detailed below, all of these paedomorphs occurred in sand or protosols of various stages of the last interglacial (MIS 5).

Two other paedomorphic forms that Gould (1969) named, *P. b. siegmundi* and *P. b. sieglindae*, were both considered by Gould to come from what was then called the Harrington Formation, which in Gould's own sequence (1969: 414, tab. 1) was attributed to the last interglacial period, thus directly contradicting his assertion that paedomorphs originated in glacial red soils. We collected topotypes of *P. b. siegmundi* on Ireland Island (Gould's site 10) from what we agree is a post-peak last interglacial (MIS 5e) highstand unit. These occurred in a white structureless, nearly pure carbonate 'protosol' (Vacher & Hearty, 1989) such as form during interglacials during pauses in eolian deposition when vegetation colonized dunes, and soils began to form. The incipient soil development ceased when renewed eolian activity buried the horizon. Mean A/I ratios of 0.52 ± 0.03 ($n = 6$) at Ireland Island confirm that deposition followed shortly after the peak MIS 5e highstand, not during a glacial episode and with no red soil.

Similarly, the type locality of *P. b. sieglindae* at Rocky Bay (Gould's site 44) is a protosol immediately overlying Devonshire marine deposits. A/I ratios of 0.51 ± 0.01 ($n = 2$) are equivalent to those of the Ireland Island paedomorphs, placing this taxon in the MIS 5 interglacial. Once again, no glacial period, no red soil.

Paedomorphs occur in MIS 5 interglacial deposits at several other sites as well. Samples that Gould (1969: 515) identified as *P. b. bermudensis* from his sites 11, 12, 15, 16, 21, 24, and 27 probably all fall in this category. These must therefore have evolved independently of *P. b. bermudensis*, which did not originate until the Holocene (Hearty et al., 2004). We have found two new sites near Saltus School in Hamilton and at the Shell fuel depot in St. Georges (probably the same rock unit as Gould's site 11) that yielded A/I mean values of 0.59 ± 0.02 ($n = 3$) and 0.54 ± 0.05 ($n = 3$), respectively. These values would place the paedomorphs at, or shortly after, the peak of the last interglacial (MIS 5e). Our sites increase the number of last interglacial deposits yielding paedomorphs, and extend their geographic range to central and eastern localities in Bermuda (Figure 1). Paedomorphs at Tobacco Bay (Gould site 27), also in St. Georges, occur in a protosol, but in this case are associated with

late MIS 5 interglacial Southampton eolianites, thus being somewhat younger than the others mentioned above. A/I from the site is 0.40 ± 0.03 ($n = 3$), which is correlated with the peak of the Southampton marine transgression and associated highstand sediment flux on to the island (Vacher & Hearty, 1989; Hearty et al., 1992).

In summary, all Pleistocene paedomorphs of the subgenus *Poecilozonites* occur in nearly pure carbonate (>95%) soils in deposits of the last interglacial (MIS 5). Those from the current interglacial (Holocene) occur in surface and pitfall deposits with high carbonate content (>70%). Whatever the cause may be for their paedomorphosis, it was not a result of living on "the almost totally lime-free soils" of glacial episodes (Gould 1977: 277).

CONCLUSION

A revised and much more accurate and detailed chronology of the geological deposits in which fossils occur now presents a very different picture of evolutionary sequences and events in the history of snails on Bermuda from anything envisioned by Gould. Changes in shell size and shape through the Pleistocene were rapid, repeated, and dramatic. While this new context for understanding change in Bermudan land snails should prove more instructive of evolutionary patterns than before, the underlining causes may be more difficult to discern. Calcium limitation was the only cause that Gould advanced and it became for him, to use one of his pet phrases, a *deus ex machina*. We believe that lack of sufficient calcium was probably the last problem any snail on Bermuda would ever have to face, so that other explanations will be required.

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Holoplanktonic Mollusca (Gastropoda) from the Gulf of Aqaba, Red Sea and Gulf of Aden (Late Holocene-Recent)

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Abstract. Fifteen bottom samples, two from the Gulf of Aqaba, twelve from the Red Sea proper and one from the Gulf of Aden, were analysed qualitatively for holoplanktonic Mollusca. The basic material yielded 43 taxa (14 Heteropoda, 1 Janthinidae, 20 Euthecosomata, 4 Pseudothecosomata and 4 Gymnosomata). Eighteen species are distributed all over the Red Sea (9 of them also in the Gulf of Aqaba), another 16 are present only in the southeastern part of the Red Sea, and 10 species were exclusively found in the Gulf of Aden sample. The presence of several further species in the Red Sea (1 heteropod, 4 janthinids, 1 thecosome, 2 pseudothecosomes, 3 gymnosomes and 1 nudibranch) is assumed on the basis of literature data or unpublished observations. Northward increasing salinity is considered to be the main cause for the differences in occurrence. Although all material studied originates from bottom samples, all species are considered to form part of the living holoplanktonic mollusc stock, judging on the presence of well-preserved specimens. Only epi- and mesopelagic species were found. Bathypelagic species are absent. Predominantly based on SEM-imaging additional data on morphology of especially the Heteropoda is given. Taxonomical and/or nomenclatural notes are added for several species.

Key Words: Holoplanktonic Mollusca, Holocene, distribution, systematics, Gulf of Aqaba, Red Sea, Gulf of Aden.

INTRODUCTION

The Red Sea (al-Bahr al-Ahmar, in Arabic language) is the world's northernmost tropical sea, situated in between the NE part of the African continent and the Arabic peninsula. Its length is approximately 1900 km, maximum width is around 350 km. In the NW the Red Sea is subdivided by the Sinai Peninsula into two bights, the western, relatively shallow (~75 m) Gulf of Suez, leading through the Suez Canal to the Mediterranean Sea, and the eastern, much deeper (~1850 m) Gulf of Aqaba [also referred to as Gulf of E(i)lat]. In the SE the relatively narrow (~35 km) Bab el-Mandab Strait connects the Red Sea with the Gulf of Aden and the Arabian Sea, which form part of the Indian Ocean.

Sea depth of the Red Sea proper amounts to over 2400 m in the central part, but is only ~137 m near the southern passage to the Gulf of Aden (Hanish Sill shallows). An isolated position and high temperature within tropical climate, with an average surface water temperature in the north of 26°C, in the south of 30°C (but rapidly decreasing to c. 22°C at a 'thermohalocline' at 100 m sea depth, Weikert, 1982, fig. 2), causing high evaporation, and lack of discharging rivers cause a hypersaline environment (salinity northward to over 40‰), considerably higher than that in the Gulf of Aden and the Indian Ocean (approximately 35‰). High temperature and salinity in the intermediate water column, together with reduced oxygen contents and

lack of food explain the absence of Red Sea bathypelagic species (Weikert, 1982; Hemleben et al., 1996).

Main currents in the Red Sea are influenced by monsoons (Baars et al., 1998). As a result of the wind system, surface currents flow from the Indian Ocean into the Red Sea during winter and the other way around in summer. Surface and nutrient-rich mid-level currents flow in opposite direction, resulting in an outflow of nutrients from the Red Sea during winter and its enrichment during summer (most data from Siddall et al., 2004; and Saudi Geological Survey, 2006). Sediment supply into the Red Sea is mainly by desert dust, transported by strong winds (NASA, 2006).

Geologically the Red Sea is a young (Oligo-Miocene) structure, originated as part of the Great Rift System, as a result of which the Arabian peninsula separated from the African mainland. The Red Sea was never part of the Tethyan Ocean.

An initially existing connection with the Mediterranean was lost in the Middle Miocene (Boswerth et al., 2005, fig. 11). During the Pliocene the connection with the Mediterranean was restored. Sea level fall during the Pleistocene isolated the Red Sea from the Mediterranean as well as from the Indian Ocean, afterwards only the southern connection was restored. During the last glaciation maximum, holoplanktonic organisms (nannoplankton, foraminifera and molluscs,

apart from the pteropod *Creseis* 'acicula' = *C. clava*) did not survive the increasing salinity (>55‰) in the Gulf of Aqaba and the northern part of the Red Sea (Almogi-Labin, 1982 and in litt., 2006). Afterwards, the one and only source of species immigrating into the Red Sea is the southern connection with the Indian Ocean, through the Bab-el-Mandab Strait. It seems that the Gulf of Aqaba was continuously connected during the last 150 kA with the Red Sea and the latter with the Gulf of Aden (Reiss et al., 1984).

At present, immigration of mollusc species from the Mediterranean through the Suez Canal, especially for holoplanktonic molluscs, can be neglected, as the main migration stream seems to be from the Red Sea into the Mediterranean (so-called Lessepsian species). Also, holoplanktonic molluscs are most probably not capable of surviving transportation through the shallow canal.

Thus, the Red Sea holoplanktonic mollusc fauna can be considered a young (holocene) assemblage, originated completely by immigration from Indian Ocean stock.

The extant overall Red Sea mollusc fauna is very rich and diverse in species, due to the presence of a wide variety of environments (as e.g., a complex reef ecosystem). Dekker & Orlin (2000) listed no less than 1765 species by name and referred to a large number of as yet unidentified further species. Holoplanktonic Mollusca from the Red Sea have been referred to in a number of papers, but an up to date overview or systematic revision is not available yet from this area. The recent inventory of Dekker & Orlin includes a number of holoplanktonics (Heteropoda, Atlantidae: 5 species; Janthinidae: 5 species; Thecosomata, Limacinidae: 3 species; Cavoliniidae: 9 species; Desmopteridae: 1 species; Gymnosomata, Pneumodermatidae: 1 species). It should be realised, however, that these references are predominantly concentrated from scattered literature resources and are not necessarily based on actual observations of these authors themselves.

Abbreviations:

NNM	Nationaal Natuurhistorisch Museum <i>Naturalis</i> , Leiden, The Netherlands.
RGM	Nationaal Natuurhistorisch Museum <i>Naturalis</i> , Leiden, The Netherlands, Palaeontology Department; formerly Rijksmuseum van Geologie en Mineralogie.
SMF	Senckenberg Museum, Frankfurt am Main, Germany.
ZMA	Instituut voor Systematiek & Populatiebiologie, Zoologisch Museum, University of Amsterdam, Department of Malacology.
A	long diameter of atlantid species (Janssen, in press, text-fig. 6).

H	shell height.
W	shell width.

MATERIALS AND METHODS

Fifteen bottom samples, predominantly from deep water (range 56–2120 m) and reasonably well-spread over the entire length of the Red Sea (Text-fig. 1), were analysed qualitatively for holoplanktonic Mollusca. Eight of these were donated by Dr. Frank P. Wesselingh, who joined a Meteor Red Sea and Gulf of Aden collecting trip in 1995. Samples from the same trip were described and analysed by von Rützen-Kositzkau (1999), who gave extensive additional information, especially on the benthic mollusc material. A further series of 5 Red Sea samples, collected in 1981 (1 sample Valdivia 29) and 1987 (4 samples Meteor 5), was donated by Dr. Ronald Janssen (SMF) in 1996. Two samples from the Gulf of Aqaba were made available by Dr. Ahuva Almogi-Labin (Geological Survey of Israel, Jerusalem, Israel). Locality data of these samples are summarised in Table 1. Sample locations are given in Text-fig. 1.

Most samples were collected by means of box cores that take a bottom sample to a depth of 0.50 m or (usually) less of the sea bottom sediments. The age of such box core samples, as discussed by von Rützen-Kositzkau (1999, p. 49), is no more than maximally ~6 kA (usually less) and can therefore without exception be indicated as 'Late Holocene to Recent.' Such samples, of course, give no information whatsoever on seasonal fluctuations in the holoplanktonic mollusc stock. They just indicate which species occurred at the sampling sites during the last few thousand years. As quite fresh specimens were present for all species, it may be safely assumed that they do occur in the extant assemblages, occurring in the water columns over the sampled sites.

Samples taken and donated by Frank Wesselingh were washed aboard ship on a 120 µm mesh and included small sediment samples. The Senckenberg samples were obviously sieved on a 500 µm mesh and therefore the smallest species and specimens are absent (as e.g., Gymnosomata larval shells). The Gulf of Aqaba samples were received as picked material. One of them contained only specimens >1 mm.

All samples were analysed qualitatively after being separated in sieving fractions of 2000, 1000, 500, 300, 200 and 100 µm. Isolating the smallest specimens (under 200 µm) was frequently hampered by the presence of overwhelming numbers of (mainly planktonic) Foraminifera, which made concentrating the tiny mollusc specimens laborious and very time-consuming. Therefore the coarser three or four fractions usually were inspected completely, the finer ones only partially, until no further species were found. This method gives

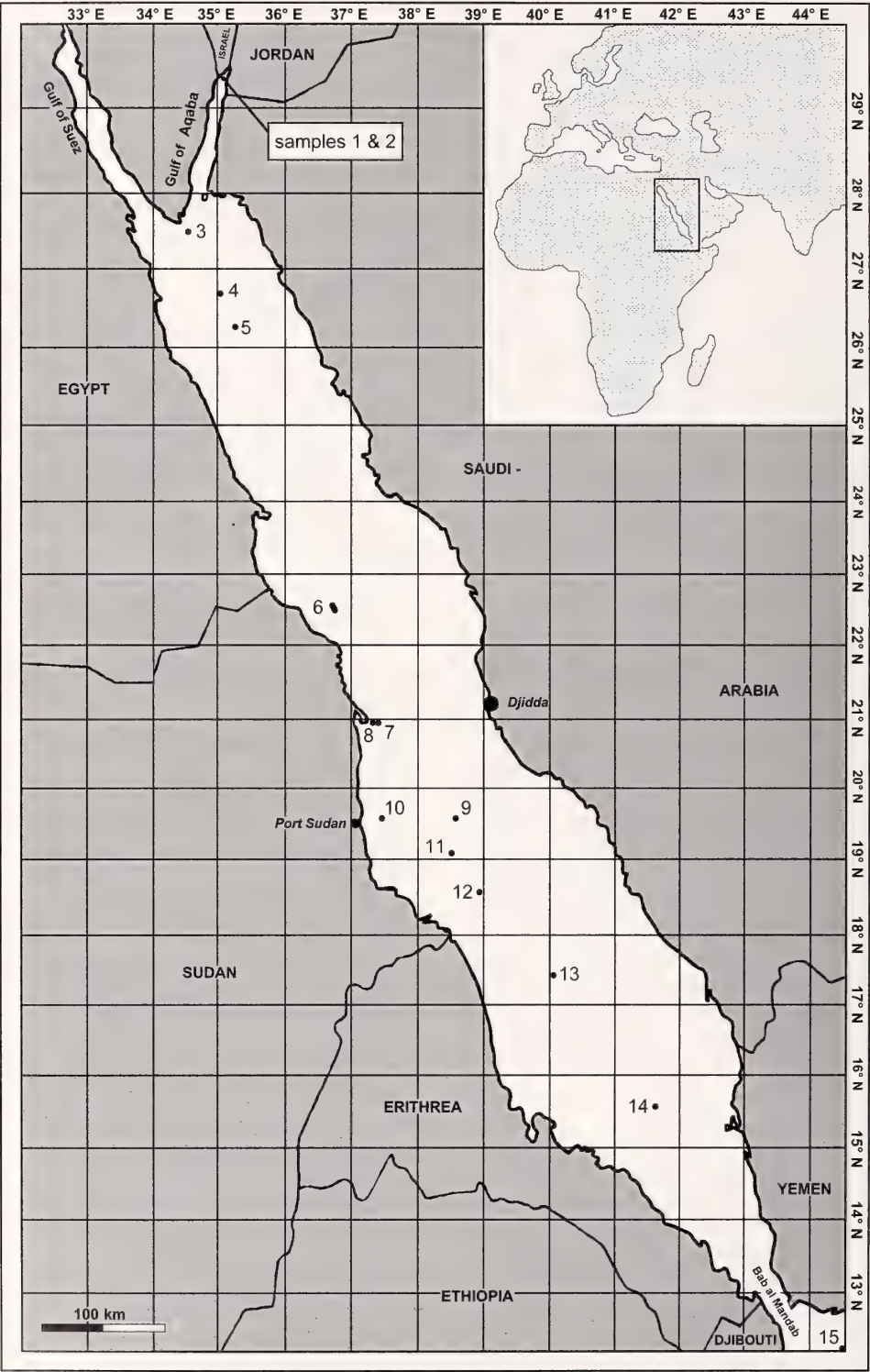


Figure 1. Location of samples (compare Table 1).

Table 1
Sample data (localities arranged from NW to SE, compare Text-fig. 1).

Nr	Locality	Coordinates	Leg.	Station	Sea depth	Date
1	Gulf of Aqaba	off Elat city	unknown	unknown	320 m	unknown
2	Gulf of Aqaba	Geziret Fara'oun 29°30'N;? E	unknown	unknown	380 m	unknown
3	Red Sea	27°41'N; 34°35'E	FS Meteor 31/2	unknown	1040 m	00.02.1995
4	Red Sea	26°44.97'N; 35°02.02'E	Valdivia 29	746 KG 873	1377 m	09.03.1981
5	Red Sea	26°14.477'N; 35°21.033'E	FS Meteor 31/2	DRZ dredge	1146 m	00.02.1995
6	Red Sea	22°35.2'–22°24.8'N to 36°45.9'–36°46.2'E	FS Meteor 5	85	772–779 m	07.02.1987
7	Red Sea	20°57.7'N; 37°25.7'E	FS Meteor 31/2	GKG 93-3	685 m	23.02.1995
8	Red Sea	20°57.5'N; 37°22.1'E	FS Meteor 31/2	GKG 93-10	56 m	23.02.1995
9	Red Sea	19°35.0'N; 38°40.0'E	FS Meteor 5	183 Ku	2120–2119 m	28.02.1987
10	Red Sea	19°33.2'N; 37°24.5'E	FS Meteor 5	196 KG	757 m	28.02.1987
11	Red Sea	19°06.3'N; 38°36.6'E	FS Meteor 31/2	GKG 100-1	393 m	27.02.1995
12	Red Sea	18°32.9'N; 38°59.4'E	FS Meteor 5	unknown	431 m	23.02.1987
13	Red Sea	17°21.7'N; 40°01.3'E	FS Meteor 31/2	MC 101-1	475 m	28.02.1995
14	Red Sea	15°33.0'N; 41°41.1'E	FS Meteor 31/2	MC 102-1	583 m	28.02.1995
15	Gulf of Aden	12°22.8'N; 44°31.5'E	FS Meteor 31/2	GKG 105-3	321 m	04.04.1995

only scant information on the relative abundance of species, the smaller forms always being underrepresented, but the numbers of specimens included in the collection (as given in Table 2) give sufficient clue in this respect.

Most material is included in the RGM collection of fossil holoplanktonic molluscs, sample 2 is housed in the Geological Survey of Israel. Registration numbers are: sample 1: RGM 540.338–540.345; sample 3: RGM 540.141–540.162; sample 4: RGM 540.163–540.190; sample 5: RGM 540.191–540.206; sample 6: RGM 517.980–518.000 and 540.135–540.140; sample 7: RGM 539.867–539.899, 540.207; sample 8: RGM 539.900–539.915; sample 9: RGM 540.080–540.111; sample 10: RGM 540.112–540.134; sample 11: RGM 540.021–540.054; sample 12: RGM 540.055–540.079; sample 13: RGM 539.960–539.993; sample 14: RGM 539.994–540.020; sample 15: RGM 539.916–539.959. All illustrated specimens separated from these samples are registered with nrs RGM 540.347–540.464.

Benthic mollusc specimens were transferred to Mr. Robert G. Moolenbeek (Zoölogisch Museum, Universiteit van Amsterdam, dept. of Malacology, Amsterdam). Teleostei otoliths found in many samples are in the collection of Mr. Kristiaan Hoedemakers (Mortsel, Belgium).

Preservation of the planktonic mollusc specimens varies from crystal clear to opaque or completely white because of recrystallisation or early stages of dissolution. In the four northwesternmost Red Sea samples (nrs 3–6), however, part of the material, sometimes even more than half the number of specimens, shows distinct dissolution of the aragonite and specimens are preserved as internal calcitic moulds, with or without their shells preserved.

Holoplanktonic molluscs (heteropods, janthinids and pteropods), concentrated from the 15 available samples, are specified in Table 2. Most species, especially so the pteropods, are well-known and sufficiently described in the existing literature, but notes on distribution, systematics and/or morphology are added below.

All SEM-images were made by the author, using the Jeol JSM-6480 LV instrument of NNM. The photographs of Plates 20–21 were kindly made by Mr Frank P. Wesselingh, with a Nikon DS-SM camera.

SYSTEMATIC PART

As synonyms for most taxa only the first valid description is given, as well as a more recent reference to a paper in which the taxon is described and well-illustrated. Extensive synonymy is to be found usually in van der Spoel (1967, 1976). For the Atlantidae some more attention is paid to the morphology of juvenile specimens, especially also by SEM-images. In particular their protoconchs are still insufficiently known, although in most cases indispensable for the recognition of the species.

Phylum Mollusca Linné, 1758
Class Gastropoda Cuvier, 1797

Note—Classification of Gastropoda, especially above the rank of superfamily, is in a 'currently very active phase of reevaluation,' as Bouchet & Rocroi (2005, p. 4) put it. To prevent the impression that the present author has a pronounced opinion on higher classification only ranks of superfamily and lower are given here.

Superfamily Pterotracheoidea Rafinesque, 1814 [= Heteropoda Lamarck, 1812 (partim); Carinarioida de Blainville, 1818]

Table 2

Holoplanktonic mollusc distribution in the Gulf of Aqaba (samples 1–2), Red Sea (samples 3–14) and Gulf of Aden (sample 15). Numbers of specimens per sample locality (m = >50 specimens).

Species	Sample														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Heteropoda															
<i>Atlanta echinogyra</i> Richter, 1972	—	—	—	—	—	—	—	—	4	1	32	—	—	10	10
<i>Atlanta frontieri</i> Richter, 1993	—	—	—	—	—	—	—	—	—	—	10	—	—	4	14
<i>Atlanta fusca</i> Souleyet, 1852	—	—	23	m	5	m	21	6	50	26	m	m	29	—	3
<i>Atlanta helicinoides</i> Souleyet, 1852	—	—	34	m	6	5	47	3	39	13	m	40	m	5	16
<i>Atlanta inclinata</i> Souleyet, 1852	6	10	m	m	m	m	m	15	m	m	m	m	m	10	20
<i>Atlanta lesueuri</i> Souleyet, 1852	—	—	—	—	—	—	—	—	39	13	m	35	m	m	19
<i>Atlanta oligogyra</i> Tesch, 1906	—	—	48	m	17	30	m	10	m	36	m	m	m	—	10
<i>Atlanta plana</i> Richter, 1972	—	—	—	1	—	12	m	—	m	m	m	m	m	m	m
<i>Atlanta turriculata</i> d'Orbigny, 1836	—	—	3	13	1	1	39	1	10	2	23	26	20	6	33
<i>Oxygyrus keraudreni</i> (Lesueur, 1817)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Carinariidae sp. 1	—	—	—	—	—	—	—	—	—	—	1	—	3	—	18
Carinariidae sp. 2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
Carinariidae sp. 3	—	—	—	—	—	—	—	—	—	—	2	—	5	—	19
<i>Pterotrachea coronata</i> Niebuhr, 1775	Red Sea, from literature data														
<i>Firolida demarestia</i> Lesueur, 1817	—	—	—	—	—	—	m	5	6	—	m	4	m	m	m
Janthinidae															
<i>Janthina exigua</i> Lamarck, 1816	Gulf of Aqaba, from literature data														
<i>Janthina janthina</i> L., 1758	Red Sea, from literature data														
<i>Janthina umbilicata</i> d'Orbigny, 1840	Red Sea, from literature data														
<i>Janthina</i> sp.	—	—	—	7	—	—	1	—	—	—	18	—	4	—	8
<i>Recluzia erythraea</i> Jickeli, 1882	Red Sea, from literature data														
Thecosomata, Euthecosomata															
<i>Heliconoides inflata</i> (d'Orbigny, 1836)	5	m	m	m	m	m	m	m	m	m	m	m	m	m	m
<i>Limacina bulimoides</i> (d'Orbigny, 1836)	—	1	m	—	m	—	m	—	50	6	m	50	40	6	m
<i>Limacina trochiformis</i> (d'Orbigny, 1836)	—	17	24	—	18	7	m	m	29	8	m	25	m	38	m
<i>Creseis chierchiai</i> (Boas, 1886)	—	—	—	—	—	—	5	—	4	2	14	5	9	6	14
<i>f. constricta</i> Chen & Bé, 1964	—	—	7	16	1	13	m	30	m	m	m	m	m	m	m
<i>Creseis clava</i> (Rang, 1828)	19	31	m	m	m	m	m	35	m	m	m	m	m	m	m
<i>Creseis conica</i> Eschscholtz, 1829	—	—	1	—	—	—	m	—	30	28	50	m	m	25	m
<i>Creseis virgula</i> (Rang, 1828)	5	7	m	m	m	m	m	70	m	m	m	m	m	12	m
<i>Hyalocylis striata</i> (Rang, 1828)	—	—	m	—	7	li	m	—	19	17	m	m	m	22	m
<i>Styliola subula</i> (Quoy & Gaimard, 1827)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3
<i>Clio (Bellardiclio) cuspidata</i> (Bosc, 1802)	—	—	—	—	—	—	—	—	—	—	—	literature data			29
<i>Clio (Clio) convexa cyphosa</i> Rampal, 2002	24	21	m	m	m	m	m	m	m	m	m	m	m	m	m
<i>Clio (Clio) pyramidata f. lanceolata</i> (Lesueur, 1813)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
<i>Cavolinia globulosa</i> (Gray, 1850)	southern Red Sea, literature data														
<i>Cavolinia uncinata</i> (Rang, 1829)	7	—	3	12	—	m	8	—	11	2	15	m	m	5	6
<i>Diacavolinia angulata</i> (Souleyet, 1852)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1
<i>Diacavolinia flexipes</i> van der Spoel et al., 1993	1	—	1	3	—	28	14	—	m	6	36	m	16	11	m
<i>Diacavolinia longirostris</i> (Blainville, 1821)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	9
<i>Diacavolinia</i> sp.	—	—	—	—	—	—	—	—	—	—	—	—	1	—	7
<i>Diacria erythra</i> van der Spoel, 1971	m	34	m	m	m	m	m	31	m	36	m	m	m	m	m
<i>Diacria quadridentata</i> (Blainville, 1821)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4
<i>Diacria trispinosa</i> (Blainville, 1821)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	3p
Cavoliniidae sp.	—	3	—	m	3	—	24	—	—	—	m	13	m	m	13
Thecosomata, Pseudothecosomata															
<i>Cymbulia sibogae</i> Tesch, 1903	southern Red Sea, literature data														
<i>Cymbulia</i> sp. 1	—	—	3	40	—	—	14	2	1	—	27	—	40	1	5
<i>Cymbulia</i> sp. 2	—	—	—	—	—	—	19	2	—	—	1	—	3	—	—
<i>Desmopterus papilio</i> Chun, 1889	southern Red Sea, literature data														
<i>Peraclis moluccensis</i> Tesch, 1903	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5
<i>Peraclis reticulata</i> (d'Orbigny, 1836)	—	—	m	m	m	m	m	1	40	40	m	31	15	—	8

Table 2
Continued.

Species	Sample														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Gymnosomata															
Gymnosomata sp. 1	—	—	—	—	—	—	43	—	5	—	36	7	m	1	8
Gymnosomata sp. 2	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
Gymnosomata sp. 3	—	—	—	—	—	—	2	—	—	—	—	—	—	—	—
Gymnosomata sp. 4	—	—	—	—	—	—	1	—	—	—	—	—	1	—	—
Gymnosomata Typ I <i>sensu</i> Kunz, 1996							Red Sea, literature data								
Gymnosomata Typ IIa <i>sensu</i> Kunz, 1996							Red Sea, literature data								
Gymnosomata Typ IIb <i>sensu</i> Kunz, 1996							Red Sea, literature data								
Nudibranchia															
<i>Glaucus atlanticus</i> Forster, 1977							southern Red Sea, K. Bandel (in litt.)								
incertae sedis															
veliger larvae?	—	—	10	—	—	—	m	9	9	—	m	—	m	m	15
'beaked larva' <i>sensu</i> van der Spoel & Newman, 1990	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—

Family Atlantidae Rang, 1829

Notes—Identification of Atlantidae species solely on shell characteristics remains hazardous. In several papers the importance of soft part anatomy (eyes, radula, operculum) is stressed and considered of utmost importance for the distinction of species, especially within the so-called 'species groups' [note the very different meaning of this wording, contrary to the same term used in the ICZN Code (1999)]. Still, careful study of especially juvenile specimens (protoconchs-1 and -2) enables recognition of the species beyond doubt in most instances, albeit that application of SEM-images usually is requisite. Specimens with missing apical whorls (which occur frequently in bottom sample material) in most cases cannot be identified with any degree of certainty.

For every species in this family one of the larger specimens is measured, giving the shell's long diameter (A), the shell height (H) and the whorl formula, as developed by Tokioka (1955), see also Janssen (in press, text-fig. 6).

Occurrences and distributions of heteropod species in the Red Sea are still largely unknown, as is clear from van der Spoel's (1976) distribution charts. The one and only heteropod species mentioned by him for the Red Sea is *Pterotrachea coronata* Niebuhr, 1775. Larval shells of that species, or even genus, were not recognised during the present study. This species was also listed by Dekker & Orlin (2000, p. 24), probably based on van der Spoel (1976).

In many atlantid species two main spirals can be distinguished on protoconch-2. One is found in the upper half of the whorls, situated at or near the place where the next whorl will attach. It separates an upper,

subsutural zone, on which further spiral lirae may be present. Sometimes the shell wall is slightly angular at this place, giving the whorl a shouldered appearance. I indicate this spiral here as 'shoulder spiral.' A further spiral is often seen lower on the whorl, separating a middle peripheral and a lower umbilical zone. This spiral develops on the teleoconch whorl into the flange-like keel, and is therefore here called the 'keel spiral.' In some species, however, one or both are entirely absent.

Genus *Atlanta* Lesueur, 1817

Type species—*Atlanta peroni* Lesueur, 1817 (Recent).

Atlanta echinogyra Richter, 1972

Pl. 1, figs. 1–3; Pl. 2, figs. 1, 2

1972 *Atlanta echinogyra* n. sp.; Richter, p. 90, figs. 3, 5, 7.

1987 *Atlanta echinogyra* Richter 1972—Richter, p. 182, pl. 1, figs. 5, 6; pl. 2, fig. 14; pl. 4, figs. 31, 32; pl. 5, figs. 36 (as *A. echinogyra*, sic!), 42; pl. 6, fig. 47; pl. 7, fig. 57.

Discussion—This species was only found in small numbers in the southeastern part of the Red Sea and in the Gulf of Aden (samples 9–15). Apparently it is sensitive for increasing salinity and therefore does not reach further to the NW.

The early protoconch whorls are ornamented with a variable number of spirals. The shoulder spiral is distinct, but may be partly covered by the next whorl. Frequently an interrupted line of slightly curved spiral segments is seen just below the shoulder spiral (Pl. 1, fig. 2a, b). The peripheral zone of the protoconch whorls is covered with regularly spaced spiral lirae

(Pl. 1, fig. 2a; Pl. 2, fig. 1). The keel spiral is weak or indicated as a slight angularity on early whorls, developing more strongly on later whorls. The base of the adult shell (Pl. 1, fig. 4) shows very fine growth-lines only. The complete protoconch, nucleus included, is covered with an extremely fine granulation (visible at magnification $c. \times 2k$, Pl. 1, figs. 2b, 3b). The spiral ornamentation on the subsutural whorl part of the protoconch is more weakly developed than in the specimen illustrated by Seapy (1990, fig. 8E–H).

Measurements of a large specimen (sample 15): $A = 1.72$ mm, $H = 0.57$ mm, whorl formula 1:0.29:0.17.

Atlanta frontieri Richter, 1993

Pl. 11, figs. 1–3

1993 *Atlanta frontieri* n.sp. Richter, p. 192, pl. 1, fig. 3; pl. 2, fig. 7, pl. 3, fig. 9, pl. 4, figs. 18, 21.

Discussion—Only juvenile specimens were found, in the southeasternmost part of the Red Sea and the Gulf of Aden (samples 11, 14 and 15). Richter recorded the species from the Indian and western Pacific oceans.

The protoconch has four whorls, together forming a low cone with concave tangents (Pl. 11, fig. 2a). The subsutural zone has a single spiral just below the suture on the earliest whorls (Pl. 11, figs. 1b, 2b, 3), and is separated by a well-developed shoulder spiral, shaped as a lamella (Pl. 11, fig. 3), and situated at or just above the place where the next whorl's suture will attach. In juvenile specimens it is visible that the shell wall is slightly angular at the place of the shoulder spiral (Pl. 11, fig. 2a). The peripheral zone is slightly convex and procured with very thin, regularly distributed spiral lirae in the smallest specimens. The keel spiral is clear, but does not cause an angularity of the shell wall. In just one specimen it can be seen that the whorl expanding rapidly is the fifth (Pl. 11, fig. 1a). These characteristics agree with *A. frontieri*, even if insufficient material is available. Also in this species the nucleus of the protoconch is very finely granulated (Pl. 11, fig. 2c).

Measurements of the largest (but still juvenile) specimen: $A = 1.22$ mm, $H = 0.56$ mm (shell height in this specimen is not, as usual, the height of the aperture, as the protoconch's apex still reaches beyond the height of the aperture), whorl formula = 1:0.38:0.22, which also indicates that the shell is still juvenile, with just half a teleoconch whorl present.

Atlanta fusca Souleyet, 1852

Pl. 2, figs. 3–5; Pl. 3, figs. 1–3

1852 *Atlanta fusca*, nobis; Souleyet, p. 389, pl. 21, figs. 15–29.

1990 *Atlanta fusca* Souleyet, 1852.—Seapy, p. 123, figs. 6G, 10A–D.

Discussion—*A. fusca* is an easily recognisable species, present in almost all samples of the Red Sea and the Gulf of Aden (except samples 1–2 and 14), sometimes in considerable numbers, even in the northwesternmost samples of the Red Sea. It is absent, however, in the Gulf of Aqaba material (but was recorded from that area by Yaron, 1977: 75). It co-occurs with the less common second species from the same species group, *A. turriculata*, in all samples. Only in the Gulf of Aden (sample 15) *A. turriculata* is more frequent than the present species.

The protoconch is relatively high conical, initially even clearly higher than wide (Pl. 2, fig. 5a). The whorls are covered with an irregular spiral ornament (Pl. 3, fig. 2a), in between which the shoulder and keel spirals sometimes are difficult to distinguish. Especially on the early whorls the spirals show a zigzag-structure (Pl. 3, fig. 1a). In adult specimens the boundary between proto- and teleoconch is distinct and situated at the place where the spiral ornament disappears (Pl. 2, figs. 3b, 4b). In fully grown specimens the spiral ornament is still visible on the umbilical side of the shell (Pl. 2, fig. 4a, b). The nucleus of the protoconch (Pl. 2, fig. 5b; Pl. 3, fig. 2b) and the early whorls (Pl. 3, fig. 1b) are covered with an extremely fine granulation (magnification $c. \times 2k$). The ultimate one third of the teleoconch separates from the penultimate whorl. Most specimens retain their reddish-brown colour.

Measurements of a large specimen (sample 12): $A = 2.16$ mm, $H = 1.00$ mm, whorl formula 1:0.32:0.14.

Atlanta helicinoides Souleyet, 1852

Pl. 3, figs. 4–6; Pl. 4, figs. 1–5

1852 *Atlanta helicinoides*, nobis; Souleyet, p. 384, pl. 20, figs. 23–30.

1987 *Atlanta helicinoides* Souleyet 1852—Richter, p. 179, pl. 1, figs. 5, 6; pl. 2, figs. 15, 16; pl. 4, figs. 31, 32; pl. 5, figs. 33, 40; pl. 6, figs. 43, 44, 51, 52, 54; pl. 7, figs. 58–60.

Discussion—Specimens of this species were isolated from all Red Sea and Gulf of Aden samples (but not from the Gulf of Aqaba), albeit sometimes in rather low numbers independent from the sampling position. Recorded alive from Red Sea plankton hauls by Bandel et al. (1997, p. 162, fig. 4G–H).

Most of the specimens still possess their original brownish colour, strongest in the larval shell part and on the keel basis. The protoconch has a regular spiral ornament all over the height of the whorl. Above the shoulder spiral, which usually is clearly recognisable (but covered by the suture of the next whorl), the ornament may be slightly weaker. The keel spiral is developed as a slight angularity around the base of the juvenile shell (Pl. 4, figs. 1a, 2) and becomes only more

significant after the boundary with the teleoconch. The spiral ornament of the shell's base is visible on the umbilical side of adult specimens (Pl. 3, fig. 6). The nucleus and early protoconch whorls are covered with an extremely fine granulation (Pl. 4, figs. 1b, 4b, c).

Very characteristic in the present material is the strikingly low keel (Pl. 3, fig. 5) of adult specimens, distinctly lower than in the specimen illustrated by Richter (1987, pl. 1, fig. 5) or even Seapy (1990, fig. 11E) and agreeing better with van der Spoel's (1976, fig. 140a, b) illustration. In several well-preserved Red Sea specimens this low keel shows short radial folds directed backward, whereas in van der Spoel's drawing these folds are perpendicular on the shell's periphery.

Richter (1987), among others, stressed the resemblance of *Atlanta inflata* Souleyet, 1852 and the present species. Still, the differences in height/width-proportions of juvenile shells (compare Richter, 1990, pl. 5, figs. 33, 34 and 37, 38) are significant and cannot be overlooked. Also the adult keel is much wider in *A. inflata* (see Seapy, 1990, fig. 11A). This latter species, however, could not be recognised in any of the samples studied here. Apparently it does not occur in the Red Sea, although the species was mentioned (but not described or illustrated) by Bandel et al. (1997, p. 162).

Measurements of a large specimen (sample 4): A = 1.72 mm, H = 0.72 mm, whorl formula 1:0.28:0.17.

Atlanta inclinata Souleyet, 1852

Pl. 5, figs. 1–5

1852 *Atlanta inclinata*, nobis; Souleyet, p. 375, pl. 19, figs. 9–15.

1990 *Atlanta inclinata* Souleyet 1852—Richter, p. 261, pl. 1, figs. 3, 4, 10; pl. 2, figs. 15, 16; pl. 3, figs. 22, 26, 30; pl. 4, figs. 32, 37, 39.

Discussion—This is the most abundant atlantid species found in the Red Sea samples, present in most samples in more than 50 specimens. It is only less common in the Gulf of Aqaba, in sample 8 (the shallowest sample, from a sea depth of just 56 m) and in samples 14 and 15, in the southwestern Red Sea and the Gulf of Aden, respectively.

The material studied here is characterised by the possession of a protoconch of 4–4¼ whorls, clearly inclined with respect to the teleoconch's axis. Identification of the species as *A. inclinata* is already apparent because of the size of the shell, reaching to over 6 mm shell width in the largest specimens from the Red Sea. In such large specimens the last complete whorl separates from the preceding one, the space is filled by the keel (Pl. 5, figs. 1, 2). On the protoconch whorls a shoulder spiral is vaguely indicated by a very slight angularity of the shell wall (Pl. 5, fig. 3), whereas the keel spiral is more significant (Pl. 5, fig. 5). The internal radial wall structure of the protoconch whorls, de-

scribed by Richter (1990, p. 261), occurring in the related species *A. inclinata* and *A. tokiokai* van der Spoel & Troost, 1972, could be observed in several fresh specimens with the light microscope, but is of course invisible in a SEM-image. Dissolution of inner shell wall parts, also characteristic for these two species (Richter, 1990, pl. 3, figs. 21, 22), could only be seen in some specimens of which protoconch whorls were broken, as most specimens are insufficiently transparent or filled with matrix.

Measurements of large specimen (sample 5): A = 6.64 mm, H = 2.16 mm, whorl formula 1:0.31:0.07.

Atlanta lesueuri Souleyet, 1852

Pl. 5, figs. 6, 7; Pl. 6, figs. 1–3

1852 *Atlanta Lesueurii*, nobis; Souleyet, p. 380, pl. 20, figs. 1–8.

1990 *Atlanta lesueuri* Souleyet, 1852—Seapy, p. 118, figs. 5B, 6A, 7A–D.

Discussion—This species is a common constituent of the holoplanktonic mollusc stock in the SE part of the Red Sea and the Gulf of Aden only (samples 9–15). Further to the NW it is completely absent. It was already recorded from the Red Sea by Richter (1986, p. 21).

Atlanta lesueuri can only be confused with the other species from the same species group, *A. oligogyra* (see below). Both have a protoconch of just three whorls without any ornament, and a teleoconch rapidly increasing in width. In the former, however, the protoconch whorls are separated by incised sutures (Pl. 6, figs. 2, 3), whereas in the latter the sutures of the early whorls are superficial (Pl. 7, figs. 1–3).

Juvenile specimens of *A. plana* in the present material are easily mistaken for *A. lesueuri*, as the shape of the early whorls is quite similar. In *A. plana*, however, the protoconch has one whorl more and a distinct shoulder spiral is always present. The second and third whorl of that species bear faint spirals on the subsutural zone, sometimes difficultly seen with a normal binocular microscope, but clearly present in SEM-images. A shoulder and keel spiral are hardly or not developed in *A. lesueuri*, the lower one occasionally is visible in juvenile specimens as a very faint line (Pl. 6, fig. 3). In specimens of three or less whorls the peripheral zone of the whorls is flattened, giving the shell a more or less rectangular shape (Pl. 6, figs. 2, 3). In completely adult specimens one third of the body whorl separates from the preceding whorl.

The taxa '*Atlanta Lesueurii*' d'Orbigny, 1836 (presently *Limacina lesueuri*) and '*Atlanta Lesueurii*' Souleyet, 1852 (now *Atlanta lesueuri*) are primary homonyms (ICZN art. 53.3 and 57.2). The junior homonym, however, is not automatically to be replaced, but the

case should be referred to the Commission, for ruling under its plenary powers (ICZN art. 23.9.5) (Janssen & Seapy, in press).

Measurements of a large specimen (sample 12): A = 2.76 mm, H = 1.0 mm, whorl formula 1:0.16:0.07. In the measured specimen the last third part of the body whorl separates from the penultimate whorl.

Richter (1986, p. 22) refers to considerably larger specimens (4 mm), and Souleyet (1852, p. 381) even reported specimens with a 'diamètre antéro-postérieur' of 6 mm, but even in such large specimens only a small part of the last whorl separates from the preceding whorl. The Red Sea specimens clearly remain smaller.

Atlanta oligogyra Tesch, 1906

Pl. 6, figs. 4–7; Pl. 7, figs. 1–3

1906 *Atlanta oligogyra* n. sp.; Tesch, p. 54, pl. 8, figs. 14–18.

1990 *Atlanta oligogyra* Tesch, 1906—Seapy, p. 118, figs. 7E–H.

Discussion—*Atlanta oligogyra* is a common species in almost all samples, inclusive of the northwestern-most ones. It is absent, however, in the Gulf of Aqaba and in just one sample (nr 14) from the Red Sea proper. It is less common in the Gulf of Aden sample.

This species is distinguished from *A. lesueuri*, of the same species group, by the very superficial sutures of the earliest whorls (Pl. 7, figs. 1–3). In very juvenile specimens (less than three whorls) the shoulder and keel spirals are absent, or just barely visible as faint lines, without any further ornament being present. The shape of such juvenile shells differs significantly from *A. lesueuri* of the same size, as the peripheral zone is not flattened, but regularly curved (Pl. 7, figs. 1–3). In the largest specimens here too the last whorl separates slightly from the penultimate whorl (Pl. 6, fig. 4).

Measurements of a large specimen (sample 6): A = 2.48 mm, H = 0.96 mm, whorl formula 1:0.15:0.05.

Atlanta plana Richter, 1972

Pl. 7, fig. 4; Pl. 8, figs. 1–4; Pl. 9, fig. 1

1972 *Atlanta plana* n. sp.; Richter, p. 90, figs. 4, 6, 8.

1990 *Atlanta plana* Richter—Seapy, p. 120, figs. 3A, B, 6E, 8A–D, 9A, B.

Discussion—*Atlanta plana* is a very common species in the southeastern part of the Red Sea (samples 6 to 14) and is also present in the Gulf of Aden sample. In the more northwestern part it is virtually absent (just one specimen in sample 4). Living specimens were mentioned from the Red Sea by Bandel *et al.* (1997, p. 162).

The protoconch of this species has $3\frac{1}{4}$ rather convex whorls in a conical shape. The shoulder spiral is

distinctly present (Pl. 8, figs. 2a, 3a, 4) all over the protoconch and disappears after the boundary with the teleoconch. It is also visible in more adult specimens, but at places it can be covered by the suture of the subsequent whorl. Very juvenile shells are slightly angular on the place of the shoulder spiral. The keel spiral is much less distinct, at this place the whorl is gradually rounded. On the subsutural zone of the second and the third whorl two very fine and slightly irregular spiral lirae are present (Pl. 7, fig. 4c; Pl. 8, fig. 3b). These are sometimes difficult to be distinguished under a light microscope. In specimens of less than three whorls the peripheral zone bears regularly spaced spiral lirae (Pl. 8, figs. 2a, 3a, 4), that disappear soon adapturally. Also in this species the nucleus of the protoconch is covered with an extremely fine granulation (Pl. 8, figs. 2b, 3c).

Measurements of a large specimen (sample 10): A = 4.40 mm, H = 1.52 mm, whorl formula = 1:0.26:0.07.

Atlanta turriculata d'Orbigny, 1836

Pl. 9, figs. 2, 3; Pl. 10, figs. 1–3

1836 *Atlanta turriculata*, d'Orb.; d'Orbigny, p. 173, pl. 20, figs. 5–11.

1990 *Atlanta turriculata* d'Orbigny—Seapy, p. 123, figs. 5C, 9E, F, 10E–H.

Discussion—This species is absent in the Gulf of Aqaba, but present all over the Red Sea and in the Gulf of Aden (samples 3–15), but usually in rather low numbers. This species was recorded alive from the Red Sea by Bandel *et al.* (1997, p. 162, figs. 4E, F, 5).

The protoconch consists of *c.* $3\frac{1}{2}$ whorls. It is high conical, juvenile shells with this number of whorls (Pl. 10, fig. 3a) are twice as high as wide. The fourth and later whorls expand rapidly (Pl. 10, figs. 1, 2a), resulting in a planispiral adult shell, on which the protoconch protrudes almost as a small cylinder. The shoulder spiral is present from the first whorl onwards as a distinct carina in the middle of the protoconch whorls. It becomes less obvious only on the first rapidly widening whorl (Pl. 10, fig. 1) and after the boundary with the teleoconch. On very juvenile specimens the keel spiral is not very clear (Pl. 10, figs. 1, 3a), but gets stronger on later protoconch whorls (Pl. 10, fig. 2a). The subsutural zone of the protoconch whorls seems to be smooth under a light microscope, but sometimes has an ornament of an irregular spiral (Pl. 9, fig. 2c; Pl. 10, fig. 3a, c). The peripheral zone is ornamented with regularly spaced spiral lirae, frequently in a zigzag-shape. Also the base of the juvenile shell bears spirals, that touch the peripheral ornament at an angle (Pl. 10, fig. 3b). The complete protoconch, nucleus included, is covered with a very fine granulation (Pl. 10, figs. 2, 3). The spiral ornamentation is visible on the umbilical side of adult specimens (Pl. 9, fig. 3a, b). Most

specimens still have their original reddish-brown colour preserved.

Measurement of a large specimen (sample 11): A = 1.62 mm, H = 0.64 mm, whorl formula = 1:0.26:0.12.

Genus *Oxygyrus* Benson, 1835

Type species—*Oxygyrus inflatus* Benson, 1835 = *O. keraudreni* (Lesueur, 1817) (Recent)

Oxygyrus keraudreni (Lesueur, 1817)

1817 *A(tlanta) Keraudrenii*; Lesueur, p. 391.

1990 *Oxygyrus keraudreni* (Lesueur, 1817)—Seapy, p. 111, fig. 3E–H.

Discussion—Just a single juvenile specimen was found in the Gulf of Aden sample. The species is absent in all samples from the Red Sea proper and the Gulf of Aqaba.

The shell has a diameter of just 1.12 mm, its height is 0.80 mm. The protoconch ornament of spiral lines is rather worn, but just before the damaged apertural margin the sharp boundary with the teleoconch is well-indicated by the sudden disappearance of the spirals. A peripheral belt is clearly indicated on the body whorl, suddenly widening at the boundary with the teleoconch. The very short teleoconch shell part is smooth.

Family Carinariidae de Blainville, 1818

Genus *incertae sedis*

Carinariidae sp. 1

Pl. 11, fig. 4; Pl. 12, figs. 1, 2

Discussion—Protoconchs of Carinariidae sp. 1 were present in the Gulf of Aden sample (18 specimens), but the species does not seem to survive in the southwestern part of the Red Sea (3 protoconchs in sample 13, and just 1 in sample 11). More adult specimens or fragments were not found.

The specimens are easily recognised as a carinariid species, by their peculiar shell form: one and a half time wider than high, with the greatest width above the horizontal midline. The apical part of the shell is very slightly conical, with flat whorls, separated by superficial sutures. All specimens are of an opaque whitish colour, but the nucleus in all specimens is brown. The ornament exists of a subsutural spiral on the first two whorls, on both sides separated by a groove-like structure (Pl. 11, fig. 4b; Pl. 12, fig. 2b), disappearing adaperturally. The upper part of the first whorl in some specimens bears some radiating grooves (Pl. 11, fig. 4b). The base of the shell has distinctly radiating folds starting from the umbilicus and a not very well developed circum-umbilical spiral (Pl. 12, fig. 1a, b). The nucleus of the protoconch is beautifully granulated (Pl. 11, fig. 4b; Pl. 12, fig. 2b), markedly coarser than in the *Atlanta*-species.

Carinariid protoconchs are not very well known yet,

and no sufficiently well-preserved Recent material was available to identify the specimens to species level. None of the four Carinariidae protoconchs illustrated by Seapy & Thiriot-Quévieux (1994, figs. 2–13) resembles the present material completely. Their illustration of *Carinaria japonica* Okutani, 1955 resembles the present specimens most, but differs by more developed radiating lines on the early whorls and a much wider umbilicus.

Measurements of a large specimen (3 ¼ whorls): H = 0.69, W = 1.06, height of aperture = 0.54 mm.

Carinariidae sp. 2

Pl. 12, fig. 3

Discussion—Just a single very juvenile specimen, diameter barely more than 0.3 mm, from sample 15 (Gulf of Aden) differs from the two other Carinariidae types found by the absence of any spiral ornament on the first protoconch whorl. The surface of the nucleus is covered with a nice granulation, the separate elements of which tend to develop to spirals at the end of the first half whorl, towards the rather abrupt boundary with protoconch-2. Radiating riblets appear just behind the nucleus. This little shell might belong to the genus *Pterosoma*, as it basically agrees with the illustration of *Pterosoma planum* Lesueur, 1827 in Seapy & Thiriot-Quévieux (1994, fig. 2). It is too juvenile, however, to be identified with more certainty.

Carinariidae sp. 3

Pl. 13, figs. 1–3

Discussion—Carinariidae sp. 3 demonstrates a similar distribution as Carinariidae sp. 1: 19 protoconchs were found in the Gulf of Aden sample, and in addition, just 2 specimens in sample 11, and 5 in sample 13.

The juvenile specimens differ clearly from Carinariidae sp. 1 by their somewhat more flattened apical plane (Pl. 13, fig. 1a), the more convex whorls, separated by incised sutures, a more rounded aperture, and a weaker ornament, with a subsutural spiral and very faint radial lines on the first two whorls. Here too, the nucleus of the protoconch has a similar granulated surface (Pl. 13, fig. 2). In the shape of the shell they resemble *Pterosoma planum*, as illustrated by Seapy & Thiriot-Quévieux (1994, figs. 2–4), but in that species the first whorls have no spiral ornament, and the umbilicus is distinctly wider.

Measurements of a large specimen (3 whorls): H = 0.51 mm, W = 0.76 mm, height of aperture = 0.46 mm.

Family Pterotracheidae Rafinesque, 1814

Genus *Firoloida* Lesueur, 1817

Firoloida demarestia Lesueur, 1817

Pl. 13, figs. 4–6; Pl. 14, figs. 1, 2

1817 *Firoloida Demarestia*; Lesueur, p. 39, pl. 2, fig. 1, 1b.

1972 *Firoloida desmaresti* (sic!) Lesueur—Thiriot-Quiévreux, p. 560, pl. 6.

1976 *Firoloida desmaresti* (sic!) Lesueur, 1817—van der Spoel, p. 164, fig. 166.

1997 *Firoloida demarestia*—Bandel et al., p. 164, figs. 4I–K.

Discussion—Larval shells of this species are abundant (with hundreds of specimens in some samples, not all collected) in the southwestern part of the Red Sea and in the Gulf of Aden sample. It is absent in samples 1–6 and 10 (but in several of these the finer fractions yielding this species were absent). The species was mentioned from the Red Sea by Bandel et al. (1997).

Fully grown *Firoloida* specimens are 'naked.' The larval shell is shed at metamorphosis. These tiny little shells resemble very small naticids, are wider than high and have just slightly less than two whorls. Richter (1968, p. 379) found specimens in the Gulf of Naples (Mediterranean) with 2½ whorls. There is a clear boundary (in many specimens developed as a ridge, Pl. 13, fig. 6a, b) between the relatively voluminous protoconch-1 and the remaining shell. This embryonic part deviates from the shell's main axis (Pl. 14, fig. 4) and has just somewhat more than half a whorl. The nucleus is granulated (only visible in SEM-imaging, Pl. 13, fig. 4, 5, 6b), also beautifully illustrated by Thiriot-Quiévreux, 1972). The shell part beyond the boundary has faint growth lines.

In one of the specimens the shell's surface is covered with a typical pattern (Pl. 14, fig. 1), possibly representing a kind of bio-erosion, but it could also be a micro-ornament.

Measurements of a large specimen (sample 13) with almost 1¾ whorls: H = 0.47 mm, W = 0.56 mm, height of aperture = 0.32 mm. Franc (1949, p. 141) mentioned a shell width of 0.67 mm.

Note—This species presently usually is indicated with the name *Firoloida desmaresti*, see for instance van der Spoel (1976), Richter & Seapy (1999, p. 643) and many further papers. Tesch (1906, p. 42) referred to no less than 13 taxa within the genus *Firoloida*, among which *F. demarestia* Lesueur, *F. desmarestia* Souleyet, *F. desmarestii* Huxley and *F. desmaresti* Vayssiére. In Lesueur's original paper no indication is given after which person the species was named. Therefore, according to ICZN art. 32.5, *F. demarestia* Lesueur, 1817 cannot be considered an incorrect original spelling and must not be corrected. Even not if it is most probable that the name refers to Anselme G. Desmarest, who had been Lesueur's co-author of two previous papers (Kimberling, 2006; with a nice portrait of Lesueur). Van der Spoel (1976, p. 164), who errone-

ously cited Lesueur (1817) as *F. desmaresti*, instead of *F. demarestia*, mixed up things completely by suggesting that the spellings *F. demarestia* in Abbott (1974, p. 135) or *F. demaresti* in Franc (1949, p. 141) were 'corrections of the original misspelling.' Franc, however, did not at all use *demaresti*, both in the title and the text of his paper the name occurs as '*F. Desmaresti*!' Abbott on p. 135 used both *desmarestia* and *demarestia* and one could wonder which of the two should be considered a *lapsus*. Bandel et al. (1997) applied the correct name for this species.

Superfamily Epitonioidea Berry, 1910

Family Janthinidae Lamarck, 1822

Note—Yaron (1977: 75) referred to two samples of *Janthina exigua* Lamarck, 1816, washed ashore on Gulf of Aqaba beaches in 1976. Mienis (1987) and Mienis & Spanier (1987) mentioned specimens of *J. umbilicata* d'Orbigny, 1840 from Rass umm Sid (Sinai) in the Jerusalem collections and to (unchecked?) occurrences of *J. exigua* Lamarck, 1822 and *J. globosa* Swainson, 1822.

Dekker & de Ceuninck van Capelle, 1994 refer to two *Janthina* species from Yemen (Red Sea coast), viz. *J. janthina* and *J. umbilicata*. Henk Dekker's collection also contains a specimen of *J. umbilicata* from the Egyptian Red Sea coast (Dekker, in litt., 2006).

The genus *Recluzia*, also referred to by Mienis (1987), likewise occurs in the Red Sea, as demonstrated by a specimen of *R. erythraea* Jickeli, 1882 from the Yemen Red Sea coast, in Henk Dekker's collection. *R. erythraea* might be a younger synonym of *R. jehennei* Petit de la Saussaye, 1853.

The occurrence of *Janthina exigua*, *J. janthina*, *J. umbilicata* and *Recluzia erythraea* in the Gulf of Aqaba/Red Sea-fauna may be accepted as verified, the actual presence of *J. globosa* remains to be confirmed. Larval shells of *J. exigua* from the Red Sea were mentioned by Bandel et al. (1997), but considering the difficult identification of janthinid larval shells also this record has to be checked. In the present samples just unidentifiable remains were encountered.

Genus *Janthina* Bolten, in Röding, 1798

Type species—*Helix janthina* Linné, 1758 (Recent).

Janthina sp.

Pl. 14, figs. 3, 4

Discussion—Juvenile specimens or protoconchs were found in 5 samples (nrs 4, 7, 11, 13 and 15).

Apart from a number of isolated protoconchs just three very juvenile specimens beyond protoconch stage were found that cannot be identified to species level. Even small janthinid fragments (not collected) are easily recognisable by their purple colour.

The larval shells are oval shaped, very shiny, one and a half times higher than wide, with about $3\frac{1}{4}$ whorls, separated by superficial sutures. A slightly reinforced callus covers the umbilicus (Pl. 14, fig. 3a). The apertural margin is simple, not thickened, slightly prosocline in lateral view (Pl. 14, fig. 4a). The last two whorls of the protoconch bear a thickened spiral along the suture, accompanied by three finer spirals just below it. Around the base of the shell about four very insignificant spirals are present. Regularly spaced thin radial grooves bend slightly backward on these spirals (Pl. 14, fig. 3b). Lamellae, as described for *Janthina* sp. by Richter & Thorson (1975, p. 136), are absent. On both the palatal apertural margin and the columellar callus a structure of aragonite scales is seen (Pl. 14, figs. 3c, 4b) at strong magnification. These structures might give the living animal sufficient friction when leaving its shell (I thank Jeroen Goud at NNM for this suggestion!).

The larval shell is obliquely embedded in the first teleoconch whorl, that expands suddenly and has a v-shaped sinus in the growth lines on the middle of the whorl. Such juveniles resemble strongly the drawings given by Laursen (1953, figs. 32, 38) for *Janthina prolongata* (De Blainville, 1822) or *J. pallida* (Harvey, in Thompson, 1840). Bandel et al. (1997, p. 168, figs. 9G–K) illustrated similar janthinid larval shells from the Red Sea, which they identify as *J. exigua* Lamarck, 1816. Their specimens reach only 2.5 whorls.

Measurements of a larval shell with $3\frac{1}{4}$ whorls (sample 11): H = 0.48 mm, W = 0.38 mm, height of aperture 0.28 mm.

Thecosomata

Superfamily Limacinoidea Gray, 1847 (= Euthecosomata, pro parte)

Family Limacinidae Gray, 1847

Genus *Heliconoides* d'Orbigny, 1836

Type species—*Atlanta (Heliconoides) inflata* d'Orbigny, 1836 (Recent).

Heliconoides inflata (d'Orbigny, 1836) type B

Pl. 15, figs. 1–2

1836 *Atlanta inflata*, d'Orb.; d'Orbigny, p. 174, pl. 12, figs. 16–19.

2004 *Heliconoides inflata* (d'Orbigny, 1836) type B—Janssen, p. 110, pl. 1, figs. 4–6.

Discussion—*Heliconoides inflata* is by far the most common pteropod in the Red Sea. It is abundantly present in all samples, sometimes in many thousands of specimens. This observation is remarkable, as van der Spoel (1967, fig. 339) mentioned just one occurrence in the Red Sea, indicated by an arrow in his distribution map, suggesting an occurrence beyond its normal distribution pattern. It was, more correctly, indicated

as 'dominant' by Herman (1971, tab. 37.8). Bandel & Hemleben (1995, p. 228, figs. 1C, D, 2) reported on material from the Red Sea, giving additional information on the peculiar reproduction of this species, as earlier described by Lalli & Wells (1973), Wells (1976) and Lalli & Gilmer (1989). Also Barash & Zenziper (1994, p. 57) refer to Red Sea specimens.

Differences in the development of the apertural rostrum led Janssen (2004) to distinguish two types within *H. inflata*. In type A the subperipheral rostrum starts as a weak internal rib on early whorls and protrudes at the apertural margin. In type B a similar rostrum originates from a falciform thickening in the second half of the body whorl. At the thickening the shell is often slightly inflated, but not always.

According to these criteria all the specimens from the Red Sea and the Gulf of Aden seem to belong to type B. Not a single type A specimen was isolated, but many specimens are too opaque to observe presence or absence of an internal peripheral belt in juvenile specimens. All adult specimens with a still more or less transparent shell wall demonstrate the presence of the falciform thickening in the terminal half of the body whorl, but an outward bulging of the shell wall at the place of this thickening is only rarely present.

Specimens in internal mould preservation show the presence of the falciform thickening and the rostrum better than the very fragile specimens in shell preservation. In the latter the extremely thin shell wall above and below the rostrum invariably is broken (Pl. 15, figs. 1, 2), whereas the moulds perfectly show these shell parts. This also demonstrates that the damage of the shells is caused after sampling, by washing, sieving and/or transportation of the residues. The moulds reveal that the specimens reach the sea bottom undamaged. All internal moulds equally belong to type B.

Janssen (2004) also stated that specimens with clear coloration at the base of the shell or at the rostrum invariably belong to type A. This is contradicted by the present material, in which many sufficiently fresh type B specimens have a clear orange-brown colour spot at the beginning of the body whorl, close to the aperture.

Absence of type A specimens in the Red Sea indicates important differences in the geographical distribution of both types, but it is premature to draw taxonomical conclusions from this fact alone.

Measurement of a large specimen in internal mould preservation (sample 4): H = 1.32 mm (= height of aperture), W = 1.92 mm, number of whorls $3\frac{1}{4}$.

Genus *Limacina* Bosc, 1817

Type species—*Clio helicina* Phipps, 1774 (Recent).

Limacina bulimoides (d'Orbigny, 1836)

Pl. 15, figs. 3–5

1836 *Atlanta bulimoides*, d'Orb.; d'Orbigny, p. 179, pl. 12, figs. 36–38.

1977 *Limacina bulimoides* (d'Orbigny)—Bé & Gilmer, p. 764, pl. 3, fig. 4a–d.

Discussion—This species occurs in far lower numbers than the preceding species. It is rare or absent in some samples and common in others, independent of the sample position. The species seems to be present all over the Red Sea, inclusive of the Gulf of Aqaba (1 specimen in sample 2; see also Yaron, 1977: 76), as well as in the Gulf of Aden. Neither van der Spoel (1967, fig. 342), nor Bé & Gilmer (1977, fig. 10) knew this species to occur in the Red Sea. The former indicated only small patches of this species in the Indian Ocean. The latter authors, however, knew the species from all over the Indian Ocean, inclusive of the Gulf of Aden. Herman (1971) recorded *L. bulimoides* from glacial and post-glacial Red Sea sediments. Almogi-Labin & Reiss (1977) record the species from 'recent and subrecent sediments of the Red Sea.' Almogi-Labin (1982, fig. 3) repeated this, but did not encounter specimens in plankton hauls during the last 30 years in the Gulf of Aqaba and the northernmost Red Sea. It seems that the species disappeared 1–2 kA ago from that area. Its presence in bottom samples can be because of bioturbation (Almogi-Labin, in litt., 2007). The occurrence of fresh specimens in the present samples makes it very probable that this species still is part of the southern Red Sea holoplanktonic mollusc fauna. In the four northwest-ernmost samples the species occurs predominantly as internal moulds, with or without its shell preserved.

Adult specimens are easily recognised by their relatively high shell form and rather flat whorls, compared to *L. trochiformis*. However, very juvenile specimens are more difficult to identify. Almogi-Labin (1982, p. 56) found that they can be easily distinguished, even in specimens <300 µm, by the more depressed suture of the first whorl and the higher spire in *L. bulimoides*, which is acknowledged by the present specimens (compare Pl. 15, figs. 5a and 8–9). The nucleus of this species is covered with an irregular honeycomb micro-ornament (Pl. 15, fig. 5b) that changes on the next whorl to fine, obliquely positioned ridges. This ornament continues until the aperture, but is gradually less strongly developed.

Measurements of a large specimen (sample 12): H = 1.62 mm, W = 0.96 mm, height of aperture 0.76 mm, 6¼ whorls.

Limacina trochiformis (d'Orbigny, 1836)

Pl. 15, figs. 6–9; Pl. 16, figs. 1, 2

1836 *Atlanta trochiformis* d'Orb.; d'Orbigny, p. 177, pl. 12, figs. 29–31.

1977 *Limacina trochiformis* (d'Orbigny)—Bé & Gilmer, p. 769, pl. 3, fig. 2a–d.

Discussion—*Limacina trochiformis* is a common species all over the Red Sea, inclusive of the Gulf of Aqaba (with abundances in between those of *Heliconoides inflata* and *L. bulimoides*), in several samples occurring with hundreds of specimens. As in the case of the foregoing species neither van der Spoel (1967, fig. 341) nor Bé & Gilmer (1977, fig. 15) were aware of its presence in the Red Sea. Almogi-Labin (1982) recorded the species from plankton hauls and from Holo- and Pleistocene Red Sea sediments.

Morphologically this species is easily distinguished by its adult general shell form and convex whorls. Very juvenile specimens, however, have a less convex whorl shape (Pl. 15, figs. 8, 9) and a more superficial suture than juvenile *Limacina bulimoides* of the same size. The shell's surface has a micro-ornament of spaced oblique ridges (Pl. 15, fig. 6b). The shell wall at the palatal side of the aperture is covered with coarser and more densely placed radial ridges (Pl. 16, fig. 1a) that are composed of close-set granules (Pl. 16, fig. 1b). As in the case of *Janthina* sp. protoconchs, described above, this may provide the living animal with the necessary friction when leaving its shell.

Measurements of a large specimen (sample 4): H = 1.12 mm, W = 0.99 mm, height of aperture 0.64 mm, 5 whorls.

Superfamily Cavolinioida Gray, 1850 (= Euthecosomata, pro parte)

Family Creseidae Curry, 1982

Genus *Creseis* Rang, 1828

Type species—*Cleodora* (*Creseis*) *virgula* Rang, 1828 (Recent).

Creseis chierchiaie (Boas, 1886)

Typical form (Pl. 16, figs. 2, 3):

1886 *Cleodora Chierchia* n. sp.; Boas, p. 62, 202, pl. 3, fig. 39ter; pl. 4, figs. 43bis-ter.

1976 *Creseis chierchiaie* Boas (*sic!*) – Richter, p. 145ff, figs. 1–2.

f. *constricta* Chen & Bé, 1964 (Pl. 16, figs. 4, 5):

1964 *Creseis virgula constricta*, n. subsp.; Chen & Bé, p. 194, figs. 3d, 4d.

1977 *Creseis virgula* (Rang) *constricta* Chen and Bé – Bé & Gilmer, p. 776, pl. 5, fig. 12a, b.

See Janssen (in press) for extensive synonymy.

Discussion—The typical form of this species occurs in low numbers between the f. *constricta*, in the southeastern part of the Red Sea and the Gulf of Aden (samples 7 and 9–15). Forma *constricta* is present in all samples except those from the Gulf of Aqaba, and is especially abundant in the southeastern part of the Red Sea (samples 7–15). Almogi-Labin (1982, fig. 3; pl. 2, figs. 4, 5) found this species in early Holocene sediments and also Rampal (2002, p. 236) recorded specimens of both forms from the Red Sea.

Frontier (1965) convincingly argued that typical *C. chierchiae* and '*C. virgula constricta*' were connected in his material with numerous transitional forms and belong to the same species, viz. *C. chierchiae*. Richter (1976) demonstrated beyond doubt that *C. chierchiae* is an independent species and not the larval shell part of *Hyalocylis striata*, as postulated by van der Spoel (1967, fig. 42) and van der Spoel & Dadon (1999, fig. 6.50c).

Both formae are easily recognised between other species of *Creseis* by the typical shape of the protoconch, as well as by the growth pattern of the adult shell, which initially widens rather rapidly, but later on much slower, frequently becoming almost cylindrical in its apertural half. Growth lines and annulations lie slightly higher on the dorsal side of the shell. The f. *constricta* just differs from the typical form by a lack of annulations. Strong magnification ($\times 1200$) reveals the presence of an extremely fine and irregular radial striation (Pl. 16, fig. 5b).

Measurements of a large specimen (sample 10; f. *constricta*): H = 3.34 mm, W (dorsal view) = 0.69 mm, W (lateral view) = 0.66 mm.

Creseis clava (Rang, 1828)

Pl. 17, figs. 1–2

1828 *C[leodora (Creseis)] clava* N.; Rang, p. 317, pl. 17, fig. 5.

1828 *C[leodora (Creseis)] acicula* N.—Rang, p. 318, pl. 17, fig. 6.

2002 *Creseis acicula* (Rang, 1828)—Rampal, p. 231, figs. 9A–J.

In press *Creseis clava* (Rang, 1828)—Janssen, text-fig. 7; pl. 2, figs. 9a, b, 10a, b; pl. 23, figs. 7a, b, 8.

Discussion—This species is commonly known as *Creseis acicula* (Rang, 1828), see Janssen (in press) for a discussion on the correct name of this species and illustrations of the lectotype.

Creseis clava occurs abundantly in all samples. Van der Spoel (1967, fig. 343, as *C. acicula*) did not record the species from the Red Sea area, but Chen & Bé (1977, fig. 22, also as *C. acicula*) included the Red Sea in the distribution pattern. Bandel & Hemleben (1995, p. 231, figs. 4F–I, 5) described early development of this species based on specimens from the Gulf of Aden. Almogi-Labin (1982) found that '*C. acicula*' was the only surviving pteropod species after the glacial salinity maximum. The same author and Barash & Zenziper (1994, p. 59, fig.) mentioned its occurrence in the Gulf of Aqaba.

Mr. Henk Dekker (ZMA; in litt., 2006) reported a mass stranding of this species in September 1993, at Dahab, Gulf of Aqaba, with uncountable specimens washed ashore in a 1 cm thick layer. Living corals had caught numerous *Creseis* specimens, penetrating apex upward from the separate corallites.

The very elongate shell form distinguishes this species easily from other creseids. The most strongly resembling species is *C. conica*, which increases more rapidly in diameter and is usually at least slightly curved.

Measurements of a large specimen (sample 11): H = 10.68 mm, W at aperture = 1.04 mm, W of protoconch = 0.16 mm. Fragments indicate that adults of this species reach more than double this size.

Creseis conica Eschscholtz, 1829

Pl. 17, figs. 3, 4

1829 *Creseis conica*; Eschscholtz, p. 17, pl. 15, fig. 3.

1977 *Creseis virgula conica* Escholtz (*sic!*), 1829—Bé & Gilmer, p. 748, 776, pl. 5, fig. 13a–c.

Discussion—*Creseis conica* is not rare in the southeastern part of the Red Sea and the Gulf of Aden (samples 7–15), but almost absent in the northwestern part (just one specimen in sample 3, absent in 1–2, 4–6 and 8). Neither van der Spoel (1967, fig. 345) nor Bé & Gilmer (1977, fig. 21) recorded this species from the extant Red Sea fauna.

This species has frequently been misidentified as '*Creseis acicula clava*' (see Rampal, 2002, p. 233; Janssen, in press). It is easily distinguished from *C. clava* by its less elongate, almost completely straight (Pl. 17, fig. 4a) or (usually) slightly and gradually curved (Pl. 17, fig. 3a) shell, with all possible intermediates.

The curved form was described as a new subspecies by Rampal (*Creseis conica falciformis* Rampal, 2002). She admitted that intermediate forms occur, and that both have the same geographical distribution ('vivent aux même latitudes'). The fact, however, that these forms in her material only rarely occur at the same collecting station made her conclude on 'deux entités morphologiquement proches qui doivent répondre à des caractéristiques environnementales différentes' (two morphologically close units that must respond to different environmental features). It is difficult to imagine what ecological diversity within the same water bodies might cause the existence of two subspecies within this holoplanktonic organism. Until more evidence on such differences will be presented I see no reason to maintain two subspecies.

Measurements of a large specimen (sample 13): H = 7.97 mm, W at aperture = 1.18 mm, W of protoconch 0.09 mm.

Creseis virgula (Rang, 1828)

Pl. 17, figs. 5, 6

1828 *C[leodora (Creseis)] virgula* N.; Rang, p. 316, pl. 17, fig. 2.

1977 *Creseis virgula virgula* (Rang)—Bé & Gilmer, p. 776, pl. 5, figs. 14a–c.

Discussion—This species is present and usually abundant in all samples (1–15). Rampal (1985), however, did not find this species south of 17° N. The Red Sea was not included in van der Spoel's (1967, fig. 345) distribution map of this species. It was, however, mentioned from the Gulf of Aqaba by Almogi-Labin & Reiss (1977, p. 31) and later papers of Almogi-Labin, as well as from the Red Sea by Bandel & Hemleben (1995, p. 233, figs. 6A–C), who described early development in this species.

The shape of the shell is cylindrical, with a distinct dorsal curvature in the apical part. This species has a similar protoconch as *C. conica*, but in very small specimens in which the curvature is not yet present the two can be easily distinguished by the wider apical angle of *C. virgula*. In larger specimens (H over 6 mm) the cylindrical shell part may become slightly flexuous (Pl. 17, fig. 6a).

Rampal (2002, p. 234) introduced a new subspecies, *Creseis virgula frontieri* Rampal, 2002. As distinguishing character she mentioned the larger size (H = 8–11.5 mm), compared to *C. v. virgula* (H = 4–6 mm). The new subspecies was found in a part of the equatorial zone of the African Atlantic.

In the present Red Sea material numerous specimens reach over the size of 6 mm, and several specimens, predominantly those in internal mould preservation of the northwesternmost Red Sea samples, reach distinctly over 10 mm. Especially these larger specimens also show, what Rampal called 'une légère concavité ventrale dans la moitié antérieure,' described above as 'slightly flexuous.' Obviously such size differences belong within the normal range of variability of *C. virgula* and there is no need to distinguish a separate subspecies based on that character. Apparently Rampal's stations are situated at localities with favourable circumstances for the species, where a higher number of specimens can reach large sizes.

Measurements of a large specimen in shell preservation (sample 12): H = 8.38 mm, W at aperture = 1.26 mm, W of protoconch tip = 0.07 mm. Specimens in internal mould preservation (sample 3) reach a size of more than 11 mm, but cannot be measured accurately because of missing protoconchs and/or apertural margins.

Genus *Hyalocyclus* Fol, 1875

Type species—*Cleodora* (*Creseis*) *striata* Rang, 1828 (Recent).

Hyalocyclus striata (Rang, 1828)

Pl. 18, figs. 1–5

1828 *C[leodora (Creseis)] striata* N.; Rang, p. 315, pl. 17, fig. 3.

1977 *Hyalocyclus striata* (Rang)—Bé & Gilmer, p. 770, pl. 5, fig. 9a, b.

Discussion—This species occurs all over the Red Sea, but in variable numbers. It is common in the northwesternmost Red Sea sample 3, and absent or rare in samples 1–2, 4–6 and 8. More to the southeast it increases in abundance. Van der Spoel (1967, fig. 347) did not include the Red Sea in the distribution pattern of *H. striata*. Bé & Gilmer (1977, fig. 16) indicate it as common, which agrees with my findings. Bandel & Hemleben (1995) also studied Red Sea material of this species (see below).

The transverse ornament of the present species allows an immediate identification. The only other creseid with such annulations is *C. chierchiaie*, which is much smaller, almost straight and far more slender. Strong magnification ($\times 1000$) reveals the presence of an extremely fine longitudinal micro-ornament in between the annulations (Pl. 18, fig. 5b).

Curious is the fact that not a single protoconch of *H. striata* could be recognised in the present samples, not even in the finest fractions. Embryo's of *Hyalocyclus striata* were already nicely illustrated by Fol (1875, p. 177, pl. 5, figs. 2–4). The larval shell in these drawings is schematically outlined. Pelseneer (1888, p. 54, pl. 2, fig. 3) gave another schematical representation of the larval shell, basically agreeing with that of Fol.

In spite of these references the larval shell of *Hyalocyclus* remained largely unknown, which tempted van der Spoel (1967, fig. 42) to consider *Creseis chierchiaie* to be the larval shell of *Hyalocyclus striata*. Richter (1976) convincingly demonstrated this to be erroneous and illustrated a real, but damaged *Hyalocyclus* protoconch, fairly well agreeing with the illustrations of Fol and Pelseneer.

Almogi-Labin (1982, p. 58, pl. 1, fig. 16) even referred to 'many young shells which seem to represent the early stages of this species.' Her illustration indeed resembles the ones given by the earlier authors. It remains curious, however, that in the present material (with in several samples abundant adult specimens) not a single protoconch could be traced. An explanation is provided by Bandel & Hemleben (1995, p. 231, fig. 4E). In larval specimens caught alive in the Red Sea they observed 'shrunken and wrinkled remains of a purely organic embryonic shell' and 'the early organic portions of the shell decreased in volume and became wrinkled. This pattern was preserved due to mineral layers added from the inside.' In addition, they observed that 'the apex is usually discarded after some shell growth, and a solid rounded septum in the apical portion of the shell tube is formed.'

Rare specimens with a closed and wrinkled apical portion (Pl. 18, fig. 3a, b), as well as specimens with a septum (Pl. 18, figs. 4, 5a) are indeed found in the

present Red Sea samples. A similar specimen was already illustrated by Tesch (1904, p. 27, pl. 1, fig. 16), who also gave a drawing (fig. 17) of a specimen with its embryonic shell, differing though from Fol and Pelseneer's illustrations. A further specimen was illustrated by Kunz (1996, pl. 11, figs. 4, 5).

By far the most specimens in the present samples, however, do not show these structures, the apical shell part being just a simple opening. In such specimens apparently the larval shell remained organic and present in the living animal (as a necessary protection against infections). After death such an organic structure would disappear rapidly, leaving an empty shell with an apical opening. Obviously, only in cases where the organic tissue already tends to dissolve during life the animal would be forced to close the opening, either by precipitation of calcium carbonate as a consolidation at the inner side of the organic tissue, or by closing the opening with a septum. Apparently calcification of the original protoconch shape occurs only rarely, or is influenced by local circumstances, which would explain the many specimens referred to by Almogi-Labin.

Measurements of a large specimen (in internal mould preservation, sample 3): H = 6.81 mm, W at aperture 2.24 mm, dorso-ventral diameter at aperture = 1.70 mm, number of annulations c. 40.

Genus *Styliola* Gray, 1850

Type species—*Cleodora subula* Quoy & Gaimard, 1827 (Recent).

Styliola subula (Quoy & Gaimard, 1827)

1827 *Cleodora subula*; Quoy & Gaimard, p. 233, pl. 8D, figs. 1–3.

1999 *Styliola subula* (Quoy & Gaimard, 1827)—Janssen, p. 18, pl. 3, figs. 7–9 (with neotype designation).

For extensive synonymy see Janssen (1990, p. 32, pl. 5, figs. 13–19, pl. 6, figs. 1–9).

Discussion—This species is absent from all Gulf of Aqaba and Red Sea samples and was only found in just three specimens in the sample from the Gulf of Aden. Almogi-Labin (1982, p. 58, fig. 3) recorded the species as a fossil, mainly from interglacial periods in the Gulf of Aqaba, northernmost and central Red Sea (compare also Almogi-Labin et al., 1998, p. 104).

Family Cliidae Jeffreys, 1869

Genus *Clio* Linné, 1767

Type species—*Clio pyramidata* Linné, 1767 (Recent)

Subgenus *Bellardiclio* Janssen, 2004

Type species—*Clio (Bellardiclio) cuspidata* (Bosc, 1802) (Recent)

Clio (Bellardiclio) cuspidata (Bosc, 1802)

1802 *Hyalæa cuspidata*; Bosc, p. 241, pl. 9, figs. 5–7.

1977 *Clio cuspidata* (Bosc)—Bé & Gilmer, p. 781, pl. 5, fig. 15a–d.

Discussion—Absent in all samples from the Gulf of Aqaba and the Red Sea, but not rare in the Gulf of Aden (sample 15), from which 29 specimens were isolated. The species was also not recorded from Holocene and Pleistocene samples in the Gulf of Aqaba and the northernmost Red Sea by Almogi-Labin (1982).

Bandel & Hemleben (1995, p. 231) recorded living embryonic individuals of *Clio cuspidata*, caught in the southern Red Sea. As this species is common in the Gulf of Aden larvae obviously are transported northward. None of these, however, was found in the Red Sea samples studied here.

Subgenus *Clio* s. str.

Clio (Clio) convexa cyphosa Rampal, 2002

Pl. 19, figs. 1–4

2002 *Clio convexa cyphosa* n. ssp.; Rampal, p. 240, figs. 16A–E, 23A–B.

In press *Clio convexa cyphosa* Rampal, 2002—Janssen, pl. 3, fig. 4, fig. 2.

Discussion—This species is common in all samples (1–15) investigated, sometimes occurring in thousands of specimens. It is the secondmost abundant species, after *Heliconoides inflata*. Almogi-Labin (1982, fig. 3; pl. 2, figs. 6, 7) listed it (as *Clio convexa*) from plankton hauls and from Quaternary sediments in the Gulf of Aqaba and the northernmost Red Sea. Also Yaron (1977, p. 76) and Barash & Zenziper (1994, p. 59, fig., as *C. pyramidata*) recorded specimens from the Gulf of Aqaba. Rampal (2002) mentioned the species from just one locality in the southeasternmost part of the Red Sea (Bab el Mandeb). Bandel & Hemleben (1995, p. 230, figs. 4C, D) described larval development of this species.

The hump-backed shape of the dorsal side in lateral view (Pl. 19, fig. 2) is the distinguishing character of this subspecies, compared to the nominal subspecies (occurring all over the indo-pacific tropics and subtropics), in which the dorsal profile is gradually curved. *C. c. cyphosa* is the only form occurring in the Red Sea, but it is also present in the Gulf of Aden sample, in which *C. convexa* s. str., however, was not found. So obviously it is not restricted to the Red Sea proper. SEM-imaging ($\times 500$) reveals the presence of longitudinal striae at the boundary of protoconch and teleoconch (Pl. 19, figs. 3b, 4b).

Measurements of a large specimen (sample 15): H = 7.14 mm, W at aperture = 4.81, dorso-ventral diameter = 2.99 mm; protoconch H = 0.36 mm, W = 0.24 mm.

Clio (Clio) pyramidata Linné, 1767 forma *lan-
ceolata* (Lesueur, 1813)

- 1813 *Hyalea lanceolata*; Lesueur, p. 285, pl. 5, fig. 3.
 1967 *Clio pyramidata* Linnaeus, 1767 forma *lanceolata* Lesueur, 1813 (*sic!*)—van der Spoel, p. 68, fig. 51a–c (with extensive synonymy).

Discussion—Just a single fragmentary specimen was found in the Gulf of Aden (sample 15). Herman (1971, tab. 35.9) and Barash & Zenziper (1994, p. 59), however, mentioned this species (as *Clio pyramidata*) from the Red Sea, probably misidentifications of *Clio convexa*. The species is absent from all Red Sea samples studied for the present paper.

Family Cavoliniidae Gray, 1850

Genus *Cavolinia* Abildgaard, 1791

Type species—*Anomia tridentata* Niebuhr, 1775 (Recent).

Cavolinia globulosa (Gray, 1850)

- 1985 *Cavolinia globulosa*. Rampal, p. 267.

Note: The only record of this species is by Rampal, who found it in very low numbers in plankton hauls from the southern Red Sea. The species is absent from all samples studied here.

Cavolinia uncinata (d'Orbigny, 1836)

Pl. 20, fig. 1

- 1836 *Hyalea uncinata*, Rang; d'Orbigny, p. 93.
 1846 *Hyalea uncinata*, Rang—d'Orbigny, pl. 5, figs. 11–15.
 1969 *Cavolinia uncinata* (Rang, 1829)—van der Spoel, p. 190, fig. 2A, B (with lectotype designation).

Discussion—This large species occurs in most samples (absent only in samples 2, 5 and 8) in reasonable numbers, sometimes even more than 50 specimens. Engel & van Eeken (1962) recorded the species from Eilat (1949). Van der Spoel's (1967, fig. 359) distribution map indicates its presence only in the northernmost Red Sea, inclusive of Gulf of Aqaba and Gulf of Suez. Singer (1994b, p. 8) reported on a mass stranding ('hundreds of millions') of this species in the Gulf of Aqaba.

Van der Spoel (1967, p. 97), probably misled by earlier authors, cited Rang (1829, p. 114) as the original description of *Cavolinia uncinata*, which is incorrect. In Rang's paper the name *Hyalea uncinata* only occurs as an example of a '1er Groupe Globulosæ' within *Hyalea*, without any specific description. D'Orbigny (1836, p. 93) cited '*Hyalea uncinata*, Rang, pl. inéd.' as a synonym, from which I understand that only an unpublished illustration existed at the time, and no description. In his text d'Orbigny (p. 94) wrote: 'Nous sommes le premier à le décrire et à le publier. On voit cependant que son nom est donné par M. Rang. C'est en effet lui qui l'a nommée, dans une monographie inédite. La figure qu'il en donne représente l'animal

avec des appendices latéraux très-longs.' Inevitably, d'Orbigny, 1836 has to be considered the author of *C. uncinata*. The lectotype, however, was selected from Rang's original material (van der Spoel, 1969, p. 191, fig. 2A–B), housed in MNHN. To maintain its status as the lectotype it should be demonstrated that Rang's specimens were syntypes, i.e., that d'Orbigny included them in *H. uncinata*. As apparently d'Orbigny had access to Rang's manuscript it seems very probably that he indeed consulted Rang's material as well. Therefore ICZN art. 74.2 does not apply. Five syntypes of d'Orbigny (1836), now paralectotypes, are available in the collections of The Natural History Museum (London, UK) (Mrs Dr Kathie Way, in litt., 2006).

Van der Spoel (1969, 1971) ultimately subdivided *Cavolinia uncinata* into two subspecies, viz. *C. uncinata uncinata*, with two formae (f. *uncinata* and f. *roperi* van der Spoel, 1969) and *C. uncinata pulsatapusilla* van der Spoel, 1971, also with two formae (f. *pulsatapusilla* and f. *pulsatoides* van der Spoel, 1971). The distribution of *C. uncinata uncinata* is given as Atlantic Ocean (f. *uncinata*), Indian and probably Pacific Ocean (f. *pulsata*) and North Atlantic Ocean (f. *roperi*). For *C. uncinata pulsatapusilla* the distribution is given as Hawakil Bay, Red Sea (f. *pulsatapusilla* s. str.) and 'near Elath,' Gulf of Aqaba (f. *pulsatoides*).

Generally speaking, the distinguishing characteristics between these formae are small and subject to considerable variability (width of aperture, coloration of shell, development of lateral spines, presence of 'hammered sculpture,' curvature of apical spine, etc.) and almost impossible to apply objectively. A quick try out of van der Spoel's (1971, fig. 4) measurements gave following results. Specimens from the Red Sea studied here (sample 6, should be *C. uncinata pulsatapusilla*, according to their locality), with measurements H = 6.3 W = 6.0, fall within the range of *C. uncinata uncinata* f. *uncinata*. Specimens from near the Canary Islands (that would according to their locality belong to f. *uncinata*), with measurements H = 8.7 W = 6.8, fall within the range of f. *pulsata*. Specimens from Indonesia (that would be *C. uncinata uncinata* f. *pulsata*, according to locality), with measurements H = 7.8 W = 5.7, fall indeed within the range of f. *pulsata*. From these results I conclude that also height and width measurements hardly give reliable results. I accept only *C. uncinata* as a species, the various formae I consider normal intraspecific variability.

Measurements of a specimen from sample 6: H = 6.39 mm, W = 5.89, dorso-ventral diameter at mid-height = 3.65 mm; a larger specimen from the Gulf of Aden (sample 15): H = 9.20 mm, W = 7.05 mm.

Genus *Diacavolinia* van der Spoel, 1987

Type species—*Cavolinia longirostris* (de Blainville, 1821) (Recent).

Note—The genus *Diacavolinia* was introduced by van der Spoel (1987, p. 78) for *Cavolinia longirostris* (de Blainville, 1821), at the time including six formae. The main reason to split *Diacavolinia* off from *Cavolinia* was the fact that in the former the protoconch-1 and -2 are thrown off, whereas they are retained in adult specimens of the latter. Van der Spoel et al. (1993) raised the six formae to species level and introduced 16 further *Diacavolinia* species and two formae.

Discriminating the various taxa within *Diacavolinia* relies on unusually small characteristics, necessitating a completely new terminology of shell parts. Van der Spoel et al. (1993) followed the tendency of many other papers of the last decades, i.e., introducing new taxa based on minor characteristics or (frequently insufficient) zoogeographical information. Generally speaking, I am inclined to accept only those species that can be separated on the basis of morphological hiatuses. In cases where gradual changes occur within populations I rather accept intraspecific variability or formae, at the most. Subspecies are to be distinguished only if morphological differences are induced by a different geographical (or stratigraphical; maybe even environmental? See above under *Creseis conica*) distribution. In the case of *Diacavolinia* one would need an enormous world-wide material (which I don't have available) to get a fair impression on the validity of all new taxa. Probably, biologists will obtain much more reliable results by DNA sequencing, eventually. The geographically very restricted material available for the present study is not suitable for a final decision whether or not 'good species' (van der Spoel, 1987, p. 78) are represented.

For a discussion on the larval development of *Diacavolinia* see below, under Cavoliniidae sp.

Diacavolinia angulata (Souleyet, 1852)

Pl. 20, fig. 2

1850 *Cavolina angulosa*—Gray, 1850, p. 8.

1852 *Hyalæa angulata*, nobis; Souleyet, p. 152, pl. 5, figs. 1–6.

1993 *Diacavolinia angulosa* (Gray, 1850)—van der Spoel et al., p. 143, figs. 18A–D, pl. 2, figs. 22, 23.

Discussion—Just a single specimen was collected from the Gulf of Aden (sample 15). Van der Spoel et al. (1993, fig. 27) recorded the species from the central Indian Ocean and western Pacific. The northwestern-most part of that area comes close to the Gulf of Aden indeed.

The name *Cavolina angulosa* was published by Gray (1850, p. 8) without description, but with reference to an as yet unpublished manuscript (cited as: 'Eydoux & Souleyet, Voy. Bonite Moll. t. 4, f. 1, 6, not described'). The reference clearly points to a manuscript, later published by Souleyet (1852, p. 152, pl. 5, figs. 1–6),

where the species was described as *Hyalæa angulata*, with the vernacular name 'Hyale angulée,' also mentioned by Gray. Obviously Gray had access to or information about Souleyet's manuscript. To be nomenclaturally available, names published before 1931 must be 'accompanied by a description or a definition of the taxon that it denotes, or by an indication' (ICZN, 1999, art. 12.1). In the absence of a description or definition of '*Cavolina angulosa*' in Gray (1850) one may wonder if the reference to 'Eydoux & Souleyet' can be accepted as an indication. But art. 12.2.1 of ICZN clearly states that only a reference to 'a previously published description' can be accepted as an indication. This makes *Cavolina angulosa* Gray, 1850 an unavailable name.

The specimen differs clearly from other *Diacavolinia* specimens in the same sample, especially by the presence of a well-developed 'outer hump,' a notch in the rostrum and by more faintly developed dorsal ribs, with almost invisible lock ribs, nicely agreeing with Richter's (1979, pl. 3, fig. 37) illustration.

Measurements of the only available specimen (sample 15): H = 3.52 mm, W = 3.24 mm, dorso-ventral diameter = 1.60 mm, W of joint = 0.92 mm.

Diacavolinia flexipes van der Spoel, Bleeker & Kobayashi, 1993

Pl. 20, fig. 3

1971 *Cavolinia longirostris* (de Blainville, 1821) forma *flexipes* n. forma—van der Spoel, p. 16, figs. 15, 16, 19, 21.

1979 *Cavolinia longirostris*, forma *flexipes*—Richter, p. 20, pl. 3, figs. 31–33.

1993 *Diacavolinia flexipes* (van der Spoel, 1971); van der Spoel, Bleeker & Kobayashi, p. 147, figs. 24A–D, pl. 2, fig. 30.

Discussion—This species is present in some specimens in samples 1 and 3 to 8, but is more common in the southeastern part of the Red Sea and in the Gulf of Aden. It is the only *Diacavolinia* species recorded for the Red Sea by van der Spoel et al. (1993, fig. 36). Many earlier authors referred to this species with the name *Cavolinia longirostris*. Barash & Zenziper (1994, p. 58) also refer to specimens from the Gulf of Suez.

Diacavolinia flexipes, according to its original description, is especially characterised by its lateral spines being strongly curved dorsally, to even perpendicular to the shells' horizontal axis, and by the absence of a notch in the rostrum. Many specimens in the Red Sea material demonstrate the curved spines distinctly, but in many other shells it is less clear. In fact all transitional forms are present from hardly bent to strongly bent dorsally. Also presence or absence of a notch in the rostrum frequently is unclear, and a matter of taste. This makes a distinction doubtful

from especially *D. longirostris* (de Blainville, 1821), as redefined in van der Spoel et al. (1993, p. 132, figs. 3A, B, pl. 1, figs. 1–4), who also included in *D. flexipes* forms with less strongly bent lateral spines and with a slight notch in the rostrum (van der Spoel et al., 1993, fig. 24C, D). Following its authors I have identified all specimens from the Red Sea proper as *D. flexipes*, but considering the present material I wonder if this taxon should be given higher rank than forma. As stated above, however, the real status of all taxa in the *Diacavolinia*-complex should be (re-)evaluated in a much wider context.

The name *flexipes* was introduced by van der Spoel, 1971 as an infrasubspecific taxon and is therefore not available as a name of the species group (ICZN, 1999, art. 10.2, 45.6.4). Although Richter (1979, p. 20) in his text used '*C. l. flexipes*' it is clear from his further text and from the explanation of his pl. 3 that he interpreted the name '*flexipes*' in an infrasubspecific sense, and therefore ICZN art. 45.6.4.1 does not apply. So, van der Spoel et al. (1993) were the first to validate the name as a taxon of the species group.

Measurements of a large specimen (sample 12): H = 7.14 mm, W = 5.98 mm, dorso-ventral diameter = 3.24 mm, W of joint = 1.00 mm.

Diacavolinia longirostris (de Blainville, 1821)

Pl. 21, fig. 1

1821 *Hyalaea longirostris*, Lesueur; de Blainville, p. 81.

1993 *Diacavolinia longirostris* (De Blainville, 1821)—van der Spoel, Bleeker & Kobayashi, p. 132, fig. 3A, B, pl. 1, figs. 1–4.

Discussion—This species, as interpreted by van der Spoel et al. (1993) is not recorded from the Red Sea, but its occurrence in the western Indian Ocean (van der Spoel et al., 1993, fig. 40) makes it probable that it is present in the Gulf of Aden. I selected a number of specimens from sample 15 (= Gulf of Aden), demonstrating the distinguishing characters of this species (notch in rostrum, only slightly curved lateral spines, etc.), but as stated before, it would not have been difficult to separate a number of very similar specimens from the samples identified *D. flexipes* above, from the Red Sea proper.

Van der Spoel et al. (1993) stated that the type material of *D. longirostris* could not be located. They interpret 'typical' *D. longirostris* as 'the taxon that is certainly not described under another name than "*longirostris*.'" In this genus, however, with so many closely resembling taxa and severe identification difficulties, it would have been common sense to designate a neotype for the type species! Also they wrote that the type locality 'is not exactly given, probably it is the Atlantic Ocean,' which is erroneous,

as de Blainville explicitly stated: 'trouvée dans l'Océan Atlantique, 22°9' de latitude.' This, fortunately, agrees quite well with the distribution map in van der Spoel et al. (1993, fig. 40), which includes the latitude of 22°9' (North!) in the western Atlantic.

Measurements of a large specimen (sample 15): H = 6.56 mm, W = 5.81 mm, dorso-ventral diameter = 3.40 mm, W of joint = 1.08 mm.

Diacavolinia sp.

Pl. 21, fig. 2

? 1993 *Diacavolinia elegans* n. sp.; van der Spoel, Bleeker & Kobayashi, p. 136, figs. 9A, B, D; pl. 1, fig. 12.

Discussion—Seven specimens were found in sample 15, one further shell was isolated from sample 13.

These specimens differ from the *Diacavolinia flexipes-longirostris*-group by their small size, short rostrum without a notch, and short lateral spines, that are only slightly curved dorsally. Applying the dichotome identification key in van der Spoel et al. (1993, p. 149) leads to the species *D. elegans* van der Spoel et al., 1993, but that species is unknown from the Indian Ocean. In their remarks to *D. elegans* the authors state: 'The present species may be rather easily confused with juveniles of other species. Presence of a fully developed lock mechanism and thickening of the ventral lip rim should be controlled to determine the adult stage of the shell before it can be identified as *D. elegans*.' The lock mechanism, however, is clearly visible in the available specimens, and in most the ventral lip is reinforced indeed. I choose to record this material in open nomenclature instead of applying the name *D. elegans*.

Measurement of a large specimen (sample 15): H = 3.90 mm, W = 3.90 mm, dorso-ventral diameter = 2.03 mm, W of joint = 0.95 mm.

Genus *Diacria* Gray, 1847

Type species—*Hyalaea trispinosa* de Blainville, 1821 (Recent)

Diacria erythra van der Spoel, 1971

Pl. 21, fig. 3; Pl. 22, figs. 2, 3

1971 *Diacria quadridentata* (de Blainville, 1821) subsp. *erythra* n. subsp. forma *erythra* n. forma; van der Spoel, p. 5, fig. 6a–c.

1982 *Diacria erythra erythra* Van der Spoel—van Leyen & van der Spoel, p. 102ff.

Discussion—This species is common to abundant in all samples (1–15), the material includes many isolated protoconchs (Pl. 22, figs. 2, 3a, b) as well.

Van der Spoel (1971) introduced *D. erythra* from the Red Sea, as a subspecies of *D. quadridentata*. Apart from the typical form he also distinguished a forma

crassa van der Spoel, 1971, which was raised to subspecies level by van Leyen & van der Spoel (1982). These authors considered *D. erythra erythra* to be a 'subfossil' distributed in the Red Sea and western Indian Ocean and *D. erythra crassa* as a Recent endemic of the Red Sea, that may have occurred, in the geological past, also in the west Indian Ocean near Madagascar. Concerning *f. crassa* van der Spoel (1971, p. 7) stated: 'the shell shape resembles that of the other formae of this species it is only an exceptionally large form.'

Measurements—In both papers referred to above measurements were used to discriminate between the various taxa, using the parameters 'shell length' (H, in this paper), 'shell width' (W), and the ratio H/W. As both *D. erythra s.str.* and *D. erythra crassa* could be expected in the present material a random sample of hundred specimens (sample 12, c. 300 km NNW of the type locality of *D. erythra*) was measured in the same way (same parameters). Also the dorso-ventral diameter was measured, as well as the distance between the lateral spines and the width of the caudal spine mark, for comparison with numerical data provided by van Leyen & van der Spoel (1982, p. 109, tab. 2).

As obviously shell size was the most important criterion to distinguish *erythra* and *crassa* measurements of H and W are given in Text-fig. 2a. The discriminating boundary of $H = 3.12$ mm, as given by van der Spoel (1971, p. 6–7), is indicated in that graph, but a clear separation in two groups is not present. According to this parameter twenty specimens would belong to *crassa*, the others to *erythra s.str.*

Shell height compared to the H/W-ratio is given in Figure 2b. Here also the boundary, as given by van der Spoel (1971, fig. 2) is indicated. He found a clear separation between both taxa, but only 7 specimens of *erythra* were measured. Ranges for the H/W-ratio according to his data are 1.19–1.39 for *erythra* and 1.09–1.29 for *crassa*. These ranges, however, are in no way recognisable in my measurements. According to his data a large number of smaller specimens, with H/W-ratio < 1.19 would thus belong to *crassa*. In my measurements the specimens that according to shell height would belong to *erythra s. str.* demonstrate a much wider variability than *crassa* and nothing in the distribution points to a separation in two groups, although it is clear that smaller specimens are much more variable in H/W-ratio than larger ones.

Dorso-ventral diameter range, as measured by van der Spoel, was 2.00–2.48 for *erythra* and 2.60–3.32 for *crassa*. As seen in Text-fig. 2c the measured specimens of sample 12 cover a total range of 1.6–2.7, and just three specimens would be sufficiently convex to belong to *crassa*. Additionally, many shells are too flat (below 2.0) even to belong to *erythra s. str.* The overall distribution of the points in Figure 2c, however, gives

no indication of two taxa present. Here the larger specimens just show a slightly wider range of variability in dorso-ventral diameter.

Width between lateral spines was not measured by the authors referred to, but van Leyen & van der Spoel (1982) repeated measurements given by Frontier (1973, p. 256), who measured specimens from near Madagascar. The range of variability found by him is given as 0.85–1.3 mm, whereas the range in my measurements (Figure 2d) is practically double, viz. 1.62–2.26 mm. The distribution curve in the stacked bar graph of Text-fig. 2d is admittedly irregular but a really clear separation is not possible.

Finally, ranges of the width of the caudal spine mark, the place where the larval shell breaks off from the teleoconch, as given by van der Spoel (1971), are 0.90–0.96 mm for *erythra* and 1.04–1.36 mm for *crassa*. The range of the sample (Text-fig. 2e) is 0.84–1.16 mm and most of the specimens fall between the ranges given by van der Spoel. The graph represents a nice, only slightly asymmetrical normal distribution curve.

From all these data I conclude that a separation of *Diacria erythra erythra* and *D. e. crassa* is purely artificial. Therefore, I indicate all specimens as *Diacria erythra*. Just one variable taxon is present in the investigated bottom sample, a result that, for sure, is true for the entire Red Sea population. It might be useful to test the above results on a population of specimens caught alive, as one of the taxa (*erythra s. str.*) was supposed to be a 'subfossil,' but I do not expect this to give spectacular results, as fresh specimens of all sizes are represented in my samples. In addition, the above results basically agree with the findings of Yaron (1978), who studied samples from the Gulf of Aqaba and the northernmost Red Sea.

According to the distribution map in van Leyen & van der Spoel (1982, fig. 8) another species, *Diacria danae* van Leyen & van der Spoel, 1982 should occur in the Red Sea. It was not recognised in the present samples, specimens with a shell height range in between 1.3 and 1.9 mm were not found.

Diacria quadridentata (de Blainville, 1821)

Pl. 21, fig. 4

1821 *Hyalaea quadridentata*, Lesueur; de Blainville, p. 81.

1971 *Diacria quadridentata* (de Blainville, 1821) subsp. *quadridentata* (de Blainville, 1821) forma *quadridentata* (de Blainville, 1821)—van der Spoel, p. 4, fig. 5

Discussion—Four specimens in sample 15 (Gulf of Aden) differ clearly from the many specimens of *D. erythra* in the same sample by their faintly developed radial ribs on the dorsal shell part and the almost complete absence of transverse striae close to the dorsal

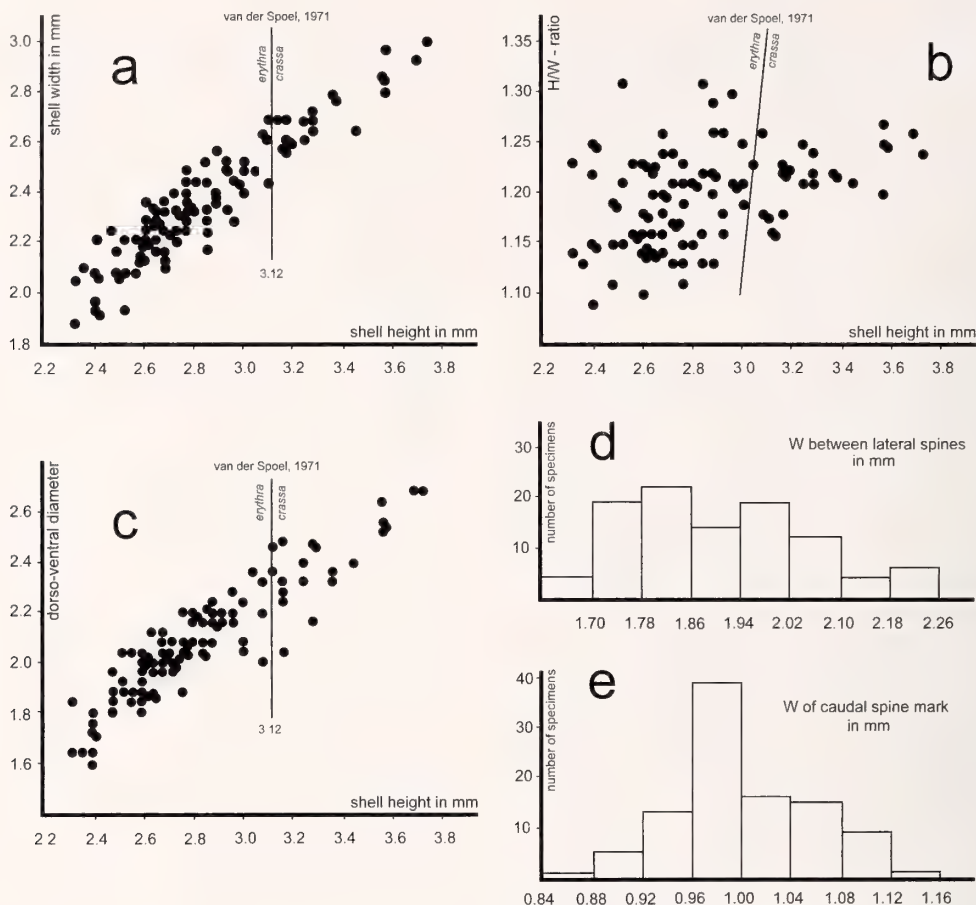


Figure 2. Measurements of 100 specimens of *Diacria erythra* (sample 12).

margin. Their measurements agree fairly well with the ranges of *D. quadridentata* (s. str.), as given by van der Spoel (1971), H of the largest specimen (3.08 mm) just exceeding the maximum value given by that author (2.9 mm), the three other specimens fit those ranges completely. The Gulf of Aden is not included in the distribution map for this species in van Leyen & van der Spoel (1982, fig. 8), but it is indicated to be present more to the South in the western Indian Ocean.

Measurements of the largest specimen: H = 3.08 mm, W = 2.56 mm, W between lateral spines = 2.24 mm, W of caudal spine mark = 1.12 mm, dorso-ventral diameter = 2.04 mm, H/W = 1.20.

Diacria trispinosa (de Blainville, 1821)

1821 *Hyalæa trispinosa*, Lesueur; de Blainville, p. 82.
1967 *Diacria trispinosa* (ms. Lesueur) (Blainville, 1821)—van der Spoel, p. 84, fig. 76a–c.

Discussion—Just three damaged larval shell parts were found in the Gulf of Aden (sample 15). The species is absent in all samples from the Gulf of Aqaba and the Red Sea proper. Bé & Gilmer (1977, fig. 28) include the Indian Ocean (apart from its central part)

with the Gulf of Aden in the distribution pattern of *D. trispinosa*. To Dupont (1979, figs. 9, 10), however, *D. trispinosa* was unknown from the northern part of the Indian Ocean. Herman (1971, tab. 35.8–9) found *D. trispinosa* in Late Glacial and Post-Glacial sediments of the Red Sea. Almogi-Labin (1982, fig. 3) recorded this species from the Gulf of Aqaba and the northernmost Red Sea in cores from the Pleistocene interglacial marine isotope stage 5. The present material indicates its rare presence in the Gulf of Aden, at least during the last few kA.

For a discussion on the validity of the many different taxa presently included in the *Diacria trispinosa*-group fide Janssen (2004). The present specimens could easily be distinguished from accompanying larval shells of the *D. quadridentata*-group, by the spherical shape of the protoconch-1.

Cavoliniidae sp. indet.

Pl. 19, fig. 5; Pl. 22, fig. 1

Discussion—In various samples studied here (see Table 2) juvenile specimens and protoconchs of Cavo-

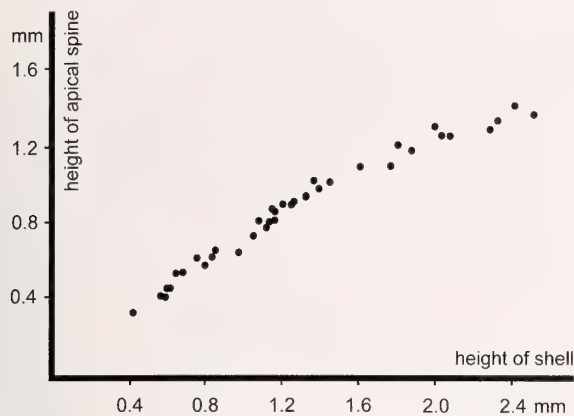


Figure 3. Measurements of Cavoliniidae sp. protoconchs (sample 11).

liniidae are common, undoubtedly belonging to either *Cavolinia uncinata* or *Diacavolinia flexipes*, as these are the only two cavoliniid species recognised. I have measured (Text-fig. 3) a number of such juvenile specimens in shell preservation in the same way as Troost & van der Spoel (1972, p. 226) indicate: apical spine height is the part of the shell posterior of the aperture. Shells were measured in dorsal view, positioning the very fragile specimens on their convex ventral side, with the dorsal apertural margin and the tip of the protoconch in focus. Thirty eight specimens, all with intact protoconch and apertural margin, and in pre-metamorphosis state, were measured.

Troost & van der Spoel found a distinct bimodality in such measurements, concluding on two species, which they identified as *Cavolinia inflexa* (Lesueur, 1813) and '*Cavolinia longirostris*.' Such a bimodality, however, is not found in my measurements, which just show a slight allometric growth, caused by the increasing size of the apertural part of the protoconchs. This might indicate that just one species is represented in this material, or that the larval shells of the two expected species (*Cavolinia uncinata* and *Diacavolinia flexipes*) do not differ in the measured parameters. Larval shells of *C. inflexa* differ clearly in shape from those of '*C. longirostris*': compare Troost & van der Spoel (1972, figs. 4a and 6c), representing specimens of 1.90 and 1.94 mm, respectively. In the former the shell is triangular, with a hardly developed apertural part, in the latter the apertural part is grown out to a half circular shape and these differences cause the bimodality in their graph.

Another Red Sea sample (nr. 3) contains many juvenile Cavoliniidae in internal mould preservation. These specimens have exactly the same shape as the specimens in the measured sample and moreover agree quite well with Troost & van der Spoel's (1993, fig. 6)

drawings of '*Cavolinia longirostris*.' Even on very small specimens in this sample the development of a stronger central and two weak lateral ribs on the dorsal side is visible. This ornament is also present on the measured specimens (compare also Pl. 22, fig. 1), but because of the lustre of the shells more difficult to observe. The internal moulds form together an ontogenetical series distinctly leading to *Cavolinia uncinata*. In the same sample a single juvenile *Diacavolinia* is present, recognisable by the shed larval shell and its joined dorsal and ventral shell walls (Text-fig. 4). In this specimen it can be seen that the radial ribs of the dorsal side start after the point where the joint is formed and that larval shells of *Diacavolinia* will not show this ornament yet. This leads to the unexpected possibility that all larval shells found in the present Red Sea samples belong to *C. uncinata*, and that the protoconch of *D. flexipes* is as yet unknown.

A larval specimen of '*C. longirostris*' with $H = 2$ mm, identified on the basis of its soft parts, was illustrated by van der Spoel (1967, figs. 230, 231). That specimen shows an almost straight shell, only very slightly curved dorsally, completely different from the specimens illustrated by Troost & van der Spoel (1972, fig. 6a–c) and the question arises if these latter authors did not study juveniles of another, real *Cavolinia*-species, instead of *Diacavolinia*!

Bandel & Hemleben (1995, p. 238, figs. 10A, B, 11A) described the development from eggs produced by mature specimens of *Diacavolinia longirostris*, caught in the Gulf of Aden. They mention the presence of a larval shell and the formation of a septum (when the shell has reached a height of about 4.8 mm) and shedding of the initial part. Interesting is the observation of demineralisation of the teleoconch after shedding, enabling deformation to the adult shell shape, after which the shell will be rapidly remineralised, fixing its new shape.

It must be kept in mind that larval shells may not be calcified at all (van der Spoel, 1967, p. 151), see also above under *Hyalocyclus striata*. If *Diacavolinia* larvae indeed have uncalcified shells (or will be decalcified anticipating shedding and metamorphosis) these will be dissolved in bottom samples, explaining their absence in the samples studied here. There is also another indication of *Diacavolinia* larval shells being uncalcified. In other pteropods shedding their larval shells (such as *Hyalocyclus*, *Cuvierina*, *Diacria*) a calcareous diaphragma (septum) is built to close the opening and invariably the place of fracture is irregular, with small fragments of the larval shell still adhering to the teleoconch (that may only disappear in fully adult specimens). In post-larval *Diacavolinia* there is no or only a very narrow septum, dorsal and ventral shell parts fit together with no opening in between and there is no trace of larval shell fragments adhering at the place of rupture.

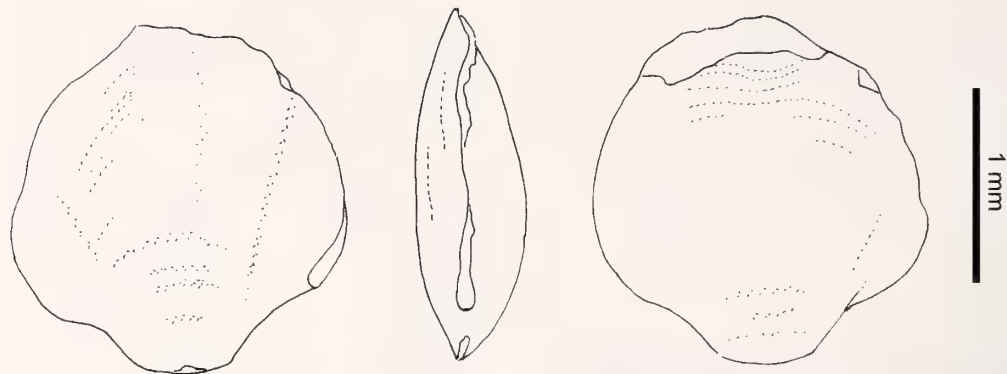


Figure 4. *Diacavolinia flexipes*, juvenile specimen in internal mould preservation (sample 12, RGM 540.157).

Van der Spoel (1987, p. 77) wrote 'In *C. longirostris* the protoconch-1 and -2 are actively thrown off when the shell is nearly full-grown and the opening in the teloconch resulting from this loss is closed by a bending of dorsal and ventral shell sides, which after their bending grow together.' This is at least partly contradicted by two juvenile specimens in the present material, one in extremely fragile shell preservation from sample 11 and one as an internal mould already mentioned above, in sample 3 (Text-fig. 4). Both specimens, H respectively 2.48 and 1.92 mm, already have their protoconchs thrown off, but dorsal and ventral shell parts of the teloconch are still flat, not yet showing the convex shapes of the fully grown specimens. This demonstrates that shedding of the larval part takes place in a rather juvenile state, and certainly not 'when the shell is nearly full-grown.'

Bandel & Hemleben (1995) demonstrated that remineralisation of the shell only takes place after shedding of the larval 'shell' and metamorphosis to the adult shell shape. This would also perfectly explain the almost seamless connection of dorsal and ventral parts after shedding.

Postlarval development of the *Diacavolinia* shell was also extensively described by Richter (1982), but he did not study the protoconch itself.

Superfamily Cymbulioidea Gray, 1840 (= Pseudothecosomata)

Family Cymbuliidae Gray, 1840

Note—Two subfamilies within the Cymbuliidae are presently distinguished, viz. Cymbuliinae and Glebinae, the former with one genus, *Cymbulia*, and three species, the latter with two genera, *Gleba* and *Corolla*, with two and five species respectively. Larval shells of *Gleba cordata* Niebuhr, 1776 were nicely illustrated in Kunz (1996, pl. 27, figs. 1–4).

Rampal (1985) recorded two species from plankton hauls in the southern Red Sea, viz. *Cymbulia sibogae* Tesch, 1903 and *Desmopterus papilio* Chun, 1889. It cannot be decided if the two forms described below

belong to these species, as their larval shells are insufficiently known. The two species recorded by Rampal are included in Table 2 as 'literature data.'

Subfamily Cymbuliinae Gray, 1840

Genus *Cymbulia* Péron & Lesueur, 1810

Type species—'Cymbulie Proboscidee' = *Cymbulia proboscidea* Lamarck, 1816 (nomen oblitum) = *Cymbulia peroni* de Blainville, 1818 (nomen protectum).

Note—Van der Spoel (1976, p. 37) wrote 'The name *C. proboscidea* Lamarck, 1816 should have priority; for stability in nomenclature, however, *C. peroni* is still used because correction would now give too many confusion.' By this statement van der Spoel obviously referred to art. 23 of the then valid second edition of the ICZN code. However, he did not, as required, refer 'the case to the Commission for a ruling.'

In the presently valid ICZN code (1999), according to art. 23.9 a ruling of the Commission is no longer necessary. According to van der Spoel's (1976) list of synonyms the last author using the name *C. proboscidea* was Woodward (1880, p. 351) which satisfies art. 23.9.1.1 ICZN. Using the same list of van der Spoel it is clear that in the period 1956–1974 at least 18 authors applied the name *C. peroni* (or *C. peronii*) as valid (satisfying art. 23.9.1.2).

In accordance with art. 23.9.2, considering the names *Cymbulia proboscidea* Lamarck, 1816 and *C. peroni* de Blainville, 1818, the younger name is here considered valid (*nomen protectum*) and the older name as invalid (*nomen oblitum*).

Cymbulia sp. 1

Pl. 22, figs. 4–6

Discussion—The minute larval shells are not rare in several samples (but of course absent in samples of which the finer fractions were not available). As Cymbuliidae are predominantly known from the living animals and/or their pseudoconchs, very little informa-

tion on the larval shell is to be found in literature. So much is clear that these larval shells have only one and a half whorl at the most, rapidly increasing in diameter, which distinguishes them from abundantly co-occurring juvenile *Heliconoides inflata* of the same size.

The present specimens are considered to belong to the genus *Cymbulia*, in which two types are distinguished. The most common of them is indicated here *Cymbulia* sp. 1. It is present in 9 of the 15 samples, sometimes with up to 40 specimens. It differs from *Cymbulia* sp. 2 in being larger and by the larger diameter of the nucleus (*c.* 0.08 mm). H of a complete shell of one whorl is *c.* 0.50 mm, shell height *c.* 0.36 mm. Its aperture is large and round. The base clearly umbilicated.

Cymbulia sp. 2

Pl. 22, figs. 7–9

Discussion—Found in four samples (nrs 7, 8, 11 and 13) in just one to three specimens, apart from sample 7, which yielded 19 specimens. They are smaller than *Cymbulia* sp. 1, but have a quarter of a whorl more. The nucleus is only *c.* 0.04 mm. One of the larger specimens measures H = 0.18 mm, W = 0.30 mm.

Family Peraclididae Tesch, 1913

Genus *Peraclis* Forbes, 1844 (emend. Pelseneer, 1888)

Type species—*Atlanta reticulata* d'Orbigny, 1836 (Recent).

Peraclis moluccensis Tesch, 1903

Pl. 23, fig. 1

1903 *Peraclis moluccensis* n. sp.; Tesch, p. 112.

1976 *Peraclis moluccensis* Tesch, 1903—van der Spoel, p. 31, fig. 12.

Discussion—Just a few damaged or juvenile specimens were found in the Gulf of Aden (sample 15). Van der Spoel's distribution map (1976, fig. 171) does not include the Gulf of Aden, but the northern limit in the Indian Ocean comes quite close to that area. Richter (1979, p. 22) did not find this species in the Indian Ocean, but reported specimens of *Peraclis apicifulva* Meisenheimer, 1906, a species not represented in my samples.

Measurements of the largest specimen: H = 1.72 mm, W = 1.74 mm, number of whorls = 2¾.

Peraclis reticulata (d'Orbigny, 1836)

Pl. 23, figs. 2, 3

1836 *Atlanta reticulata*, d'Orb.; d'Orbigny, p. 178, pl. 12, figs. 32–35, 39.

1976 *Peraclis reticulata* (d'Orbigny, 1836)—van der Spoel, p. 28, fig. 9.

Discussion—Well-preserved specimens of this species

are common in most samples, all over the Red Sea, but absent in samples 1–2 and 14 and with just 8 specimens in the Gulf of Aden sample (nr. 15). In three of the four northwesternmost samples from the Red Sea proper many specimens in internal mould preservation are present. Van der Spoel (1976, fig. 168) excluded the northern Indian Ocean (inclusive of the Red Sea) from the distribution pattern of this species. Almogi-Labin & Reiss (1977, pl. 10, fig. 4), however, recorded this species from plankton hauls, from Holocene bottom sediments and from glacial and interglacial sediments in cores in the Gulf of Aqaba and the northernmost Red Sea. Bandel & Hemleben (1995, p. 227, figs. 1A, B) described larval development of this species based on Red Sea specimens.

Peraclis reticulata is easily recognised by its sinistral, relatively high conical shell with convex whorls, on the earliest ones of which frequently the cuticulum with reticulate ornament is preserved (Pl. 23, fig. 3). The aperture is quite large, and the columella is prolonged downward into a rostrum. As the shell wall is very fragile the apertural margin is broken in all specimens, and therefore the more solid rostrum usually seems to be more prominent. On the body whorl there is a faint spiral below the upper suture. On this spiral the initially opisthocytic growth lines turn to prosoclyne, but the spiral does not develop to a spine on the apertural margin. This species does not demonstrate the radial subsutural crests as seen in other *Peraclis* species.

Measurements of a larger specimen (sample 12): H = 3.42 mm, W = 2.16 mm, number of whorls 3¾. A large specimen in internal mould preservation (sample 3) reaches a height of 3.90 mm. Van der Spoel (1976) indicates a maximum shell height of 6 mm.

Gymnosomata

Note—The Gymnosomata are a group of in the adult stage shell-less, so-called 'naked' pteropods, presently subdivided in two superfamilies, Clionoidea Rafinesque, 1815 and Hydromyloidea Pruvot-Fol, 1942. In Clionoidea four families are recognised (Clionidae, Cliopsidae, Notobrancheidae and Pneumodermatidae). In Hydromyloidea are two families, Hydromylidae and Laginiopsidae (Bouchet & Rocroi, 2005, p. 259). Altogether, some 50 species are currently accepted in the Gymnosomata (Lalli & Gilmer, 1989, p. 208).

Knipowitsch (1891) and Lebour (1931) studied the entire life cycle of a common gymnosome species, *Clione limacina* (Phipps, 1774), a coldwater species occurring in both arctic and antarctic areas. Numerous studies on anatomy, feeding and reproduction were published (for references see Lalli & Gilmer, 1989, p. 209). *C. limacina* also was the subject of a large number of neurophysiological studies in the 19-eighties and -nineties (for references see <http://www.biol.sc.edu/~vogt/courses/neuro/neurobehavior.html#clione>).

Of several gymnosome species it is known that the veliger larvae possess a shell, which is shed at the beginning of metamorphosis. Lalli & Conover (1973, 1976) studied and illustrated embryonic shells of three species, viz. *Clione limacina*, *Paedoclione doliiformis* Danforth, 1907 and *Pneumoderma atlanticum* (Oken, 1815).

Possibly most, if not all gymnosomatous species have a shell in their veliger stage, but of all the other species this shell is still unknown. Lalli & Conover (1976, p. 239) wrote 'it may be that some gymnosome species have a reduced larval shell, or none at all in free-swimming stages.' Also they state (p. 237) that 'gymnosome shells can be collected in plankton tows or bottom samples, but they often go unrecognized by planktologists and geologists.' For further discussion on gymnosomatous larval shells and their misidentification as protoconchs of the euthecosomatous pteropod *Clio polita* (Pelseneer, 1888) see Janssen (in press).

Van der Spoel & Diester-Haass (1976) also published finds of unidentified gymnosomatous larval shells, from plankton samples, as well as from ocean bottom cores off NW Africa and Portugal, sampled just below the Holocene/Pleistocene boundary. Their drawing of a fossil specimen resembles the larval shell of *Paedoclione*, as given by Lalli & Conover (1976), with which they indeed compare their specimens (misspelling the name, by the way, as *P. doliiformis*!). They concluded that they were not identical, considering differences in measurements and distribution.

In the present study four different types of gymnosomatous larval shells were found, and one of these quite abundantly. As they all basically resemble the *Paedoclione*-type they are supposed to represent species of the Clionidae family. In addition, three further gymnosomatous larval shell types from the Red Sea were recorded by Kunz (1996). They are discussed below.

Superfamily Clionoidea Rafinesque, 1815 ?

Family Clionidae Rafinesque, 1815 ?

Gymnosomata sp. 1

Pl. 23, figs. 4–7; Pl. 24, fig. 1

(1996) Gymnosomata Typ I—Kunz, p. 170, pl. 32, fig. 1 (non fig. 2).

Discussion — Specimens of this type are quite common in several samples (nrs 7, 11 and 13), rare in others (nrs 9, 12, 14 and 15) and absent in the remaining samples. Similar specimens were illustrated by Almogi-Labin & Reiss (1977, pl. 2, fig. 1) from the Gulf of Eilat and by Kunz (1996, pl. 32, fig. 1) from the Red Sea and the western Arabian Sea, respectively.

The shell consists of three parts. Total shell height reaches c. 270 µm in the largest specimens. The initial shell part (protoconch-1) is spherical and smooth ($H = 140\text{--}190\text{ }\mu\text{m}$, $W = 160\text{--}200\text{ }\mu\text{m}$), dorso-ventral di-

ameter slightly less than the shell width. After a strong constriction, in which short vertical ridges are seen, follows a further shell part (protoconch-2), shaped as an apertural collar. This collar is slightly swollen and has a smooth surface. Its central parts are slightly more produced abapically than the sides. After a sharp boundary and a slight constriction follows a third shell part clearly demonstrating growth lines (early teleoconch?). Slightly irregular longitudinal ridges are present on this latter part of the shell (magnification $\times 300$). In a lateral view (Pl. 23, fig. 7a) it is seen that the apertural margins are slightly bent together dorso-ventrally, resulting in an elliptical aperture. The shell part with growth lines sometimes is absent (Pl. 23, fig. 6, the specimen presumably died premature, before hatching or metamorphosis), or can be more or less strongly developed (Pl. 23, figs. 4a, 5a).

Closely resembling my specimens is what Kunz (1996) illustrated in his pl. 32, fig. 1, from the western Arabian Sea. That specimen differs solely by smaller dimensions and a higher and slightly more oval initial shell part. Its height reaches almost 200 µm, and shell width is 128 µm.

Gymnosomata sp. 2

Pl. 24, fig. 2

Discussion—Just a single incomplete specimen was found in sample 7. It has a preserved shell height of 200 µm and differs from the foregoing form by its relatively higher elliptical protoconch-1 shape.

Gymnosomata sp. 3

Pl. 24, fig. 3

Discussion—Of this form just two specimens were encountered in sample 7. It differs clearly and in several respects from Gymnosomata sp. 1. Its shell height reaches 262 µm, but the spherical initial part is small, with a height of c. 150 µm, and relatively higher. The constriction between protoconch-1 and the younger part of the shell is distinct. A separation between protoconch-2 and a possible early teleoconch is not clear: growth lines seem to develop immediately after the constriction. The upper half of protoconch-1 demonstrates spaced radial ridges, continuing on the lower half of the younger part of the shell, but interrupted in the constriction. At stronger magnification these ridges seem to be built up from close-set granules. A much finer and more irregular radial striation is present on the upper half of the shell part above the constriction.

Gymnosomata sp. 4

Pl. 24, fig. 4a, b

Discussion—Two specimens were found, in samples 7 and 13 one each. They agree with the general gymnosomatous shell type by being composed of

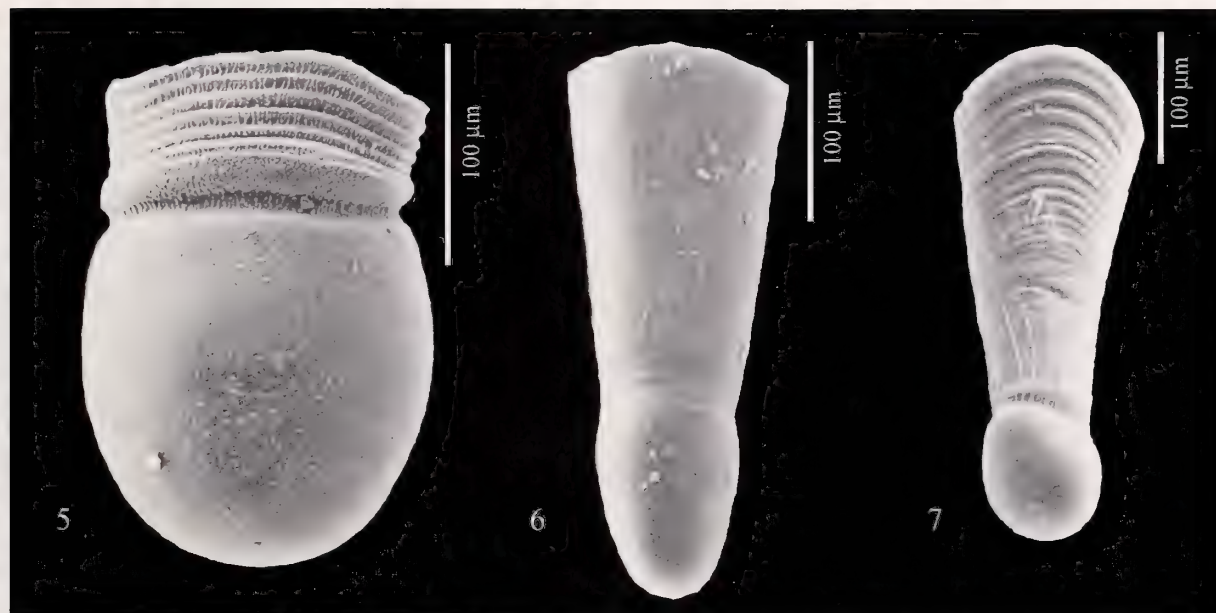


Figure 5–7. Gymnosomatous larval shells from the Red Sea (after Kunz, 1996, pl. 32, figs. 2–4). 5: *Gymnosomata* Typ I *sensu* Kunz (1996); 6: *Gymnosomata* Typ IIa *sensu* Kunz (1996); 7: *Gymnosomata* Typ IIb *sensu* Kunz (1996).

a spherical initial shell part and a cylindrical protoconch-2/teleoconch part, but the differences are obvious. The smooth protoconch-1 is small (height = 143 μm) and more elongately elliptical (width = 105 μm). The constriction between protoconchs-1 and -2 is weak and protoconch-2 is very slightly swollen. The upper boundary of this shell part (indicated by > on Pl. 24, fig. 4a) is distinct by the start of very fine longitudinal ridges (Pl. 24, fig. 4b) and growth lines. This early teleoconch part of the shell widens slightly and its surface shows irregular undulation.

Note—Kunz (1996) illustrated three further gymnomatous shells from the Red Sea (reproduced here in Text-figs. 5–7) that also have a further shell part beyond protoconch-1, but differ in details.

The specimen illustrated by Kunz (1996, pl. 32, fig. 2) resembles *Gymnosomata* sp. 1, but its third shell part shows regular transverse ribbing and more densely distributed longitudinal striation. It reaches 235 μm shell height. Presumably it does not belong to the same species. In Table 2 I indicate this form as *Gymnosomata* Typ I *sensu* Kunz (1996). His illustration is copied here as Text-fig. 5.

Gymnosomata Typ IIa (Kunz, pl. 32, fig. 3) has an oval, slightly pointed protoconch-1, a vague constriction, and a protoconch-2 that is only separated from the early teleoconch by the start of longitudinal ornament (Text-fig. 6).

Gymnosomata Typ IIb (Kunz, 1996, pl. 32, fig. 4) has a spherical protoconch-1, a clear constriction, behind

which a protoconch-2 is not very distinct. Immediately after the constriction relatively coarse and distant radial ridges develop on the early 1/3rd part of the teleoconch, which moreover is distinctly annulated (Text-fig. 7).

Superfamily *incertae sedis*

Veliger larva of unknown gastropod species?

Pl. 24, figs. 5–7

Discussion—Material of the present species is common to abundant in various samples, but is absent in samples 1–2, 4–6, 10 and 12. Bandel et al. (1997) did not record this mollusc type in their plankton hauls from the Red Sea, but Professor Klaus Bandel (in litt., 2006) told me that he did catch them indeed. At the time he suspected them to be larvae of the nudibranch *Glaucus*, but this can't be acknowledged, as the adult specimens did not reproduce and therefore their larval shell and metamorphosis could not be studied. So, these specimens still remain unidentified. In a paper by Bebbington (1986) larvae of *Glaucus atlanticus* Forster, 1777 are described, and an early shell is illustrated (Bebbington, fig. 8e), but this drawing can't be related to the present specimens.

The sinistral shells are very small ($H = c. 250 \mu\text{m}$, $W = c. 200 \mu\text{m}$) and fragile. Their overall shape is ovoid, the number of whorls is barely more than two. The apertural margin is provided with two deep circular incisions, one just below the suture, the other near the base of the shell. The incisions have a thickened margin

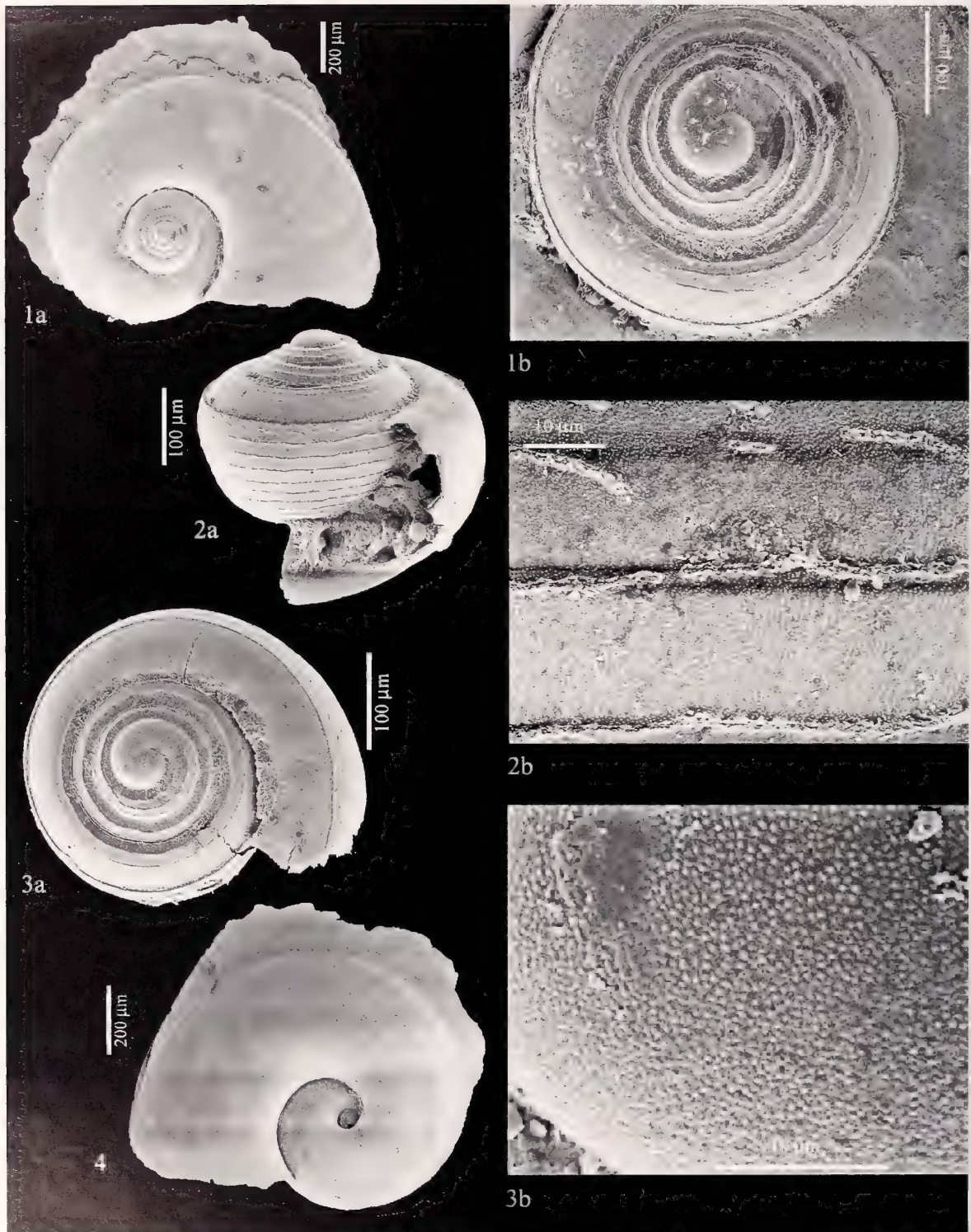


Plate 1. SEM-images of *Atlanta echinogyra* Richter, 1972 (Figures 1–4, Red Sea, sample 11, RGM 540.347–540.350). Figure 1a: adult specimen, apical view; Figure 1b: protoconch enlarged; Figure 2a: protoconch, oblique apertural/apical view; Figure 2b: micro-ornament just below the shoulder spiral; Figure 3a: protoconch, apical view; Figure 3b: micro-ornament of nucleus; Figure 4: adult specimen, umbilical view.

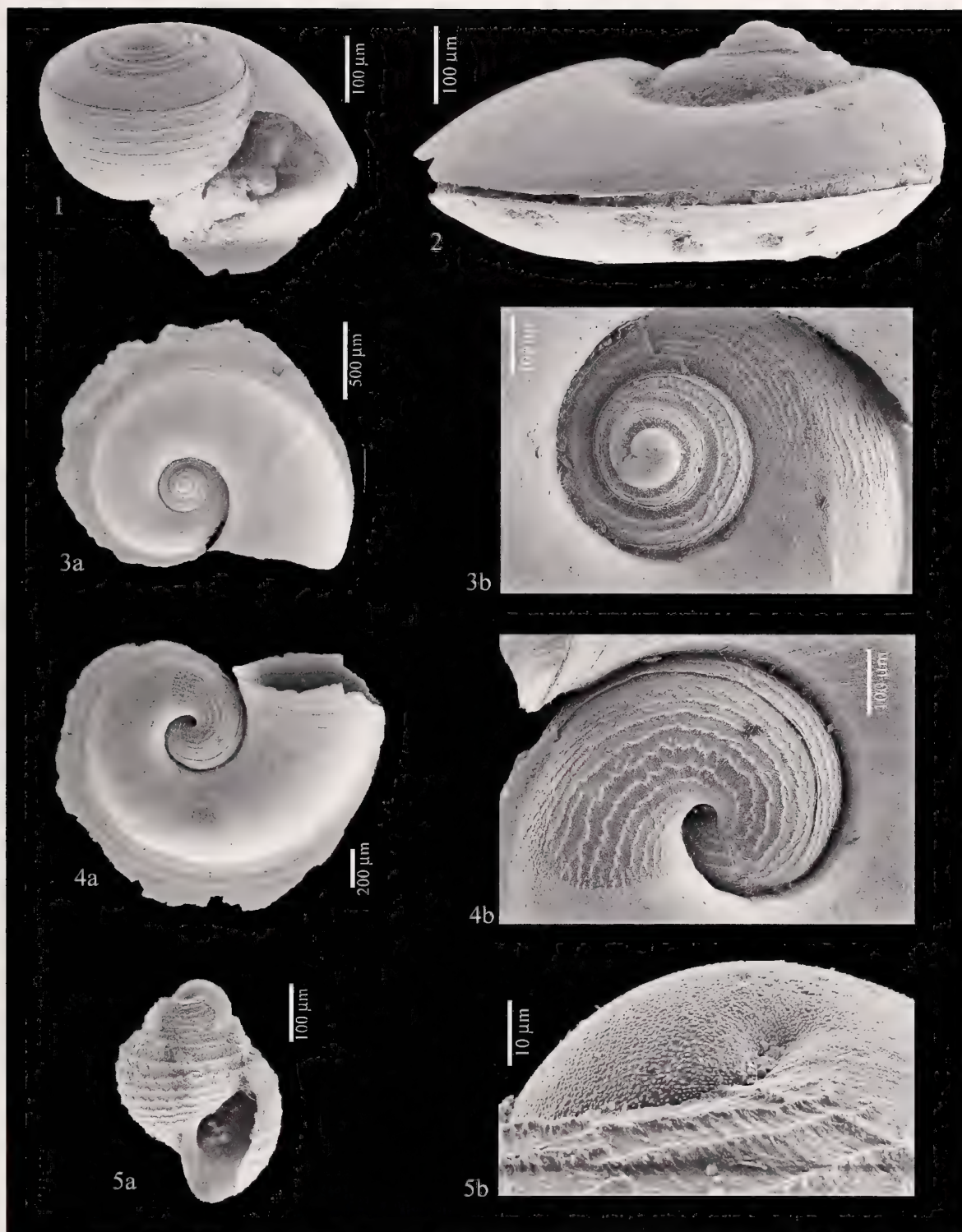


Plate 2. SEM-images of *Atlanta echinogyra* Richter, 1972 (Figures 1–2; Red Sea, sample 11, RGM 540.351–540.352) and *A. fusca* Souleyet, 1852 (Figures 3–5, Red Sea, sample 12, RGM 540.353–540.354; sample 13, RGM 540.355). Figure 1: protoconch, oblique apertural/apical view; Figure 2: adult specimen, posterior view; Figure 3a: adult specimen, apical view; Figure 3b: protoconch enlarged; Figure 4a: adult specimen, umbilical view; Figure 4b: protoconch enlarged, umbilical view; Figure 5a: protoconch, apertural view; Figure 5b: micro-ornament of nucleus.

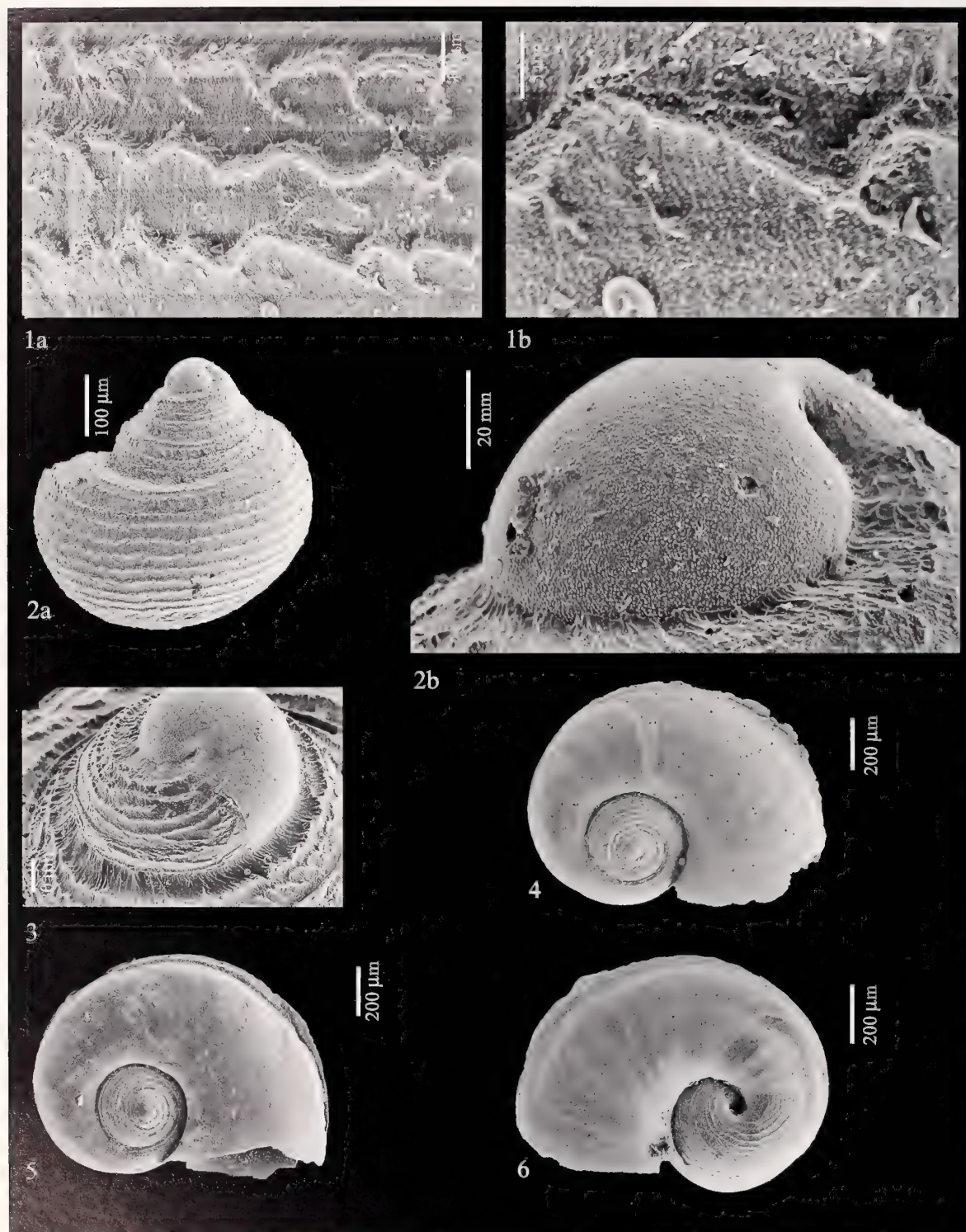


Plate 3. SEM-images of *Atlanta fusca* Souleyet, 1852 (Figures 1–3, Red Sea, sample 13, RGM 540.355–540.357) and *Atlanta helicinoides* Souleyet, 1852 (Figures 4–6, Red Sea, sample 13, RGM 540.358–540.360). Figure 1a: spirals in zigzag-shape of protoconch illustrated Pl. 2, fig. 5; Figure 1b: same, more strongly enlarged; Figure 2a: protoconch, posterior view; Figure 2b: micro-ornament of nucleus; Figure 3: nucleus and early whorl of protoconch; Figures 4, 5: adult specimens, apical views; Figure 6: adult specimen, umbilical view.

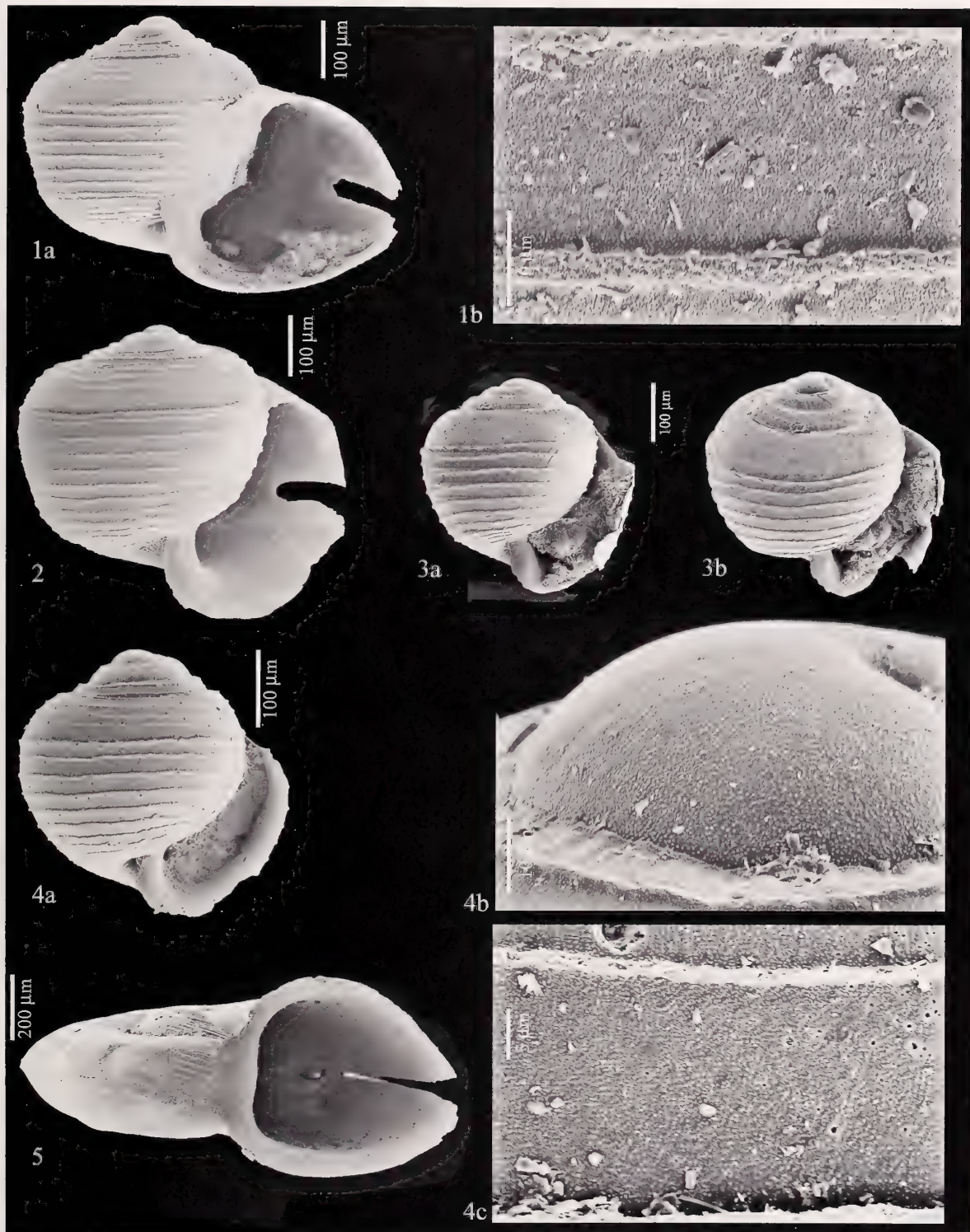


Plate 4. SEM-images of *Atlanta helicinoides* Souleyet, 1852 (Figures 1–5, Red Sea, sample 13, RGM 540.361–54.364; sample 11, RGM 540.365). Figure 1a: protoconch, apertural view; Figure 1b: micro-ornament between peripheral spirals; Figure 2: protoconch, apertural view; Figure 3a: protoconch, apertural view; Figure 3b: protoconch, oblique apertural/apical view; Figure 4a: protoconch, apertural view; Figure 4b: micro-ornament of nucleus; Figure 4c: micro-ornament between peripheral spirals; Figure 5: adult specimen, apertural view.

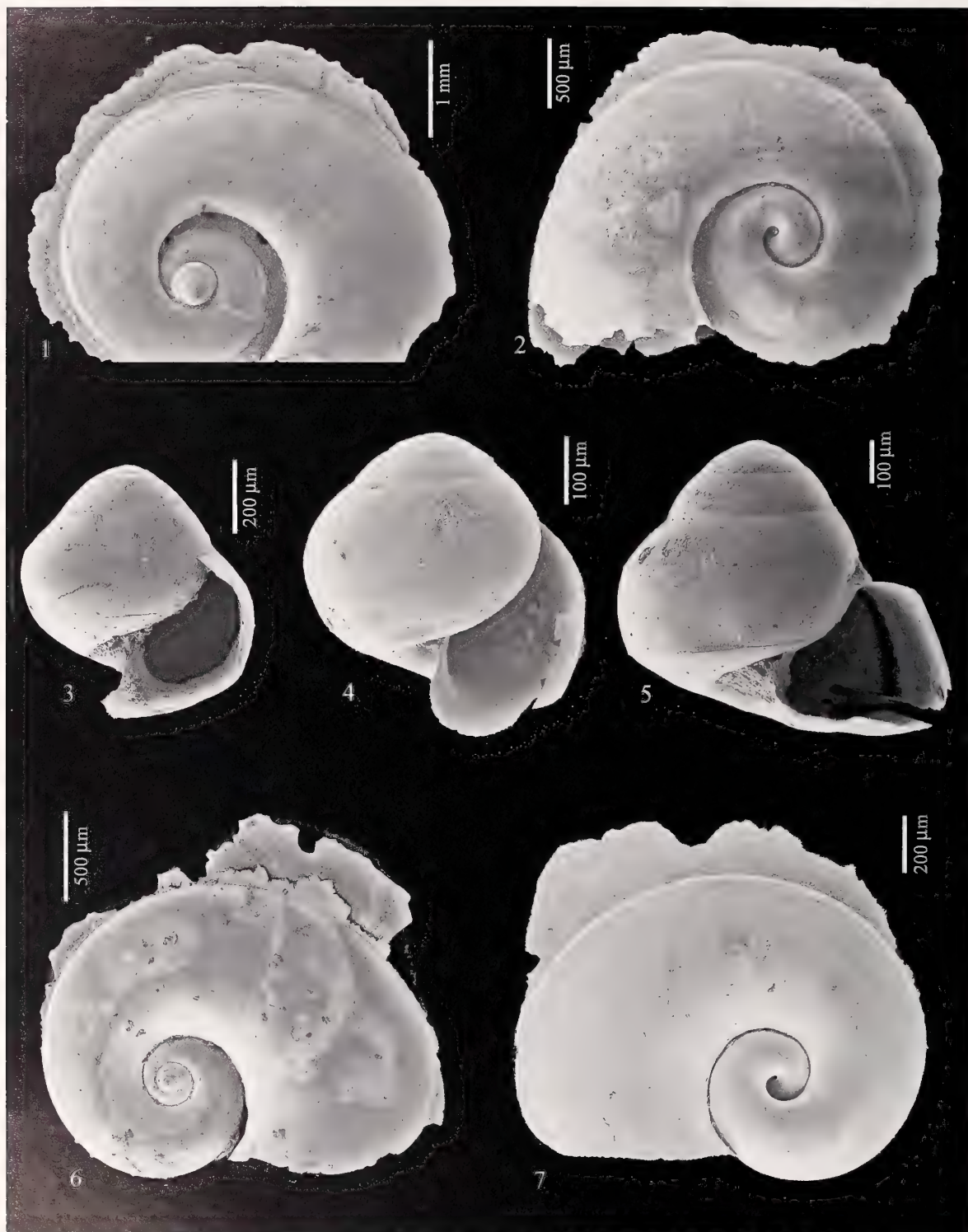


Plate 5. SEM-images of *Atlanta inclinata* Souleyet, 1852 (Figures 1–5, Red Sea, sample 13, RGM 540.366–540.370) and *A. lesueuri* Souleyet, 1852 (Figures 6, 7, Red Sea, sample 13, RGM 540.371–540.372). Figure 1: adult specimen, apical view; Figure 2: adult specimen, umbilical view; Figures 3–5: protoconchs, apertural views; Figure 6: adult specimen, apical view; Figure 7: adult specimen, umbilical view.



Plate 6. SEM-images of *Atlanta lesueuri* Souleyet, 1852 (Figures 1–3, Red Sea, sample 13, RGM 540.373–540.375) and *A. oligogyra* Tesch, 1906 (Figure 4, Red Sea, sample 6, RGM 540.376; Figures 5 and 7, Red Sea, sample 11, RGM 540.377–540.378, Figure 6, Red Sea, sample 7, RGM 540.379). Figure 1: juvenile specimen, apertural view; Figs. 2, 3: protoconchs, apertural views; Figures 4–6: adult specimens, apical views; Figure 7a: adult specimen, umbilical view; Figure 7b: umbilicus, enlargement of Figure 7a.

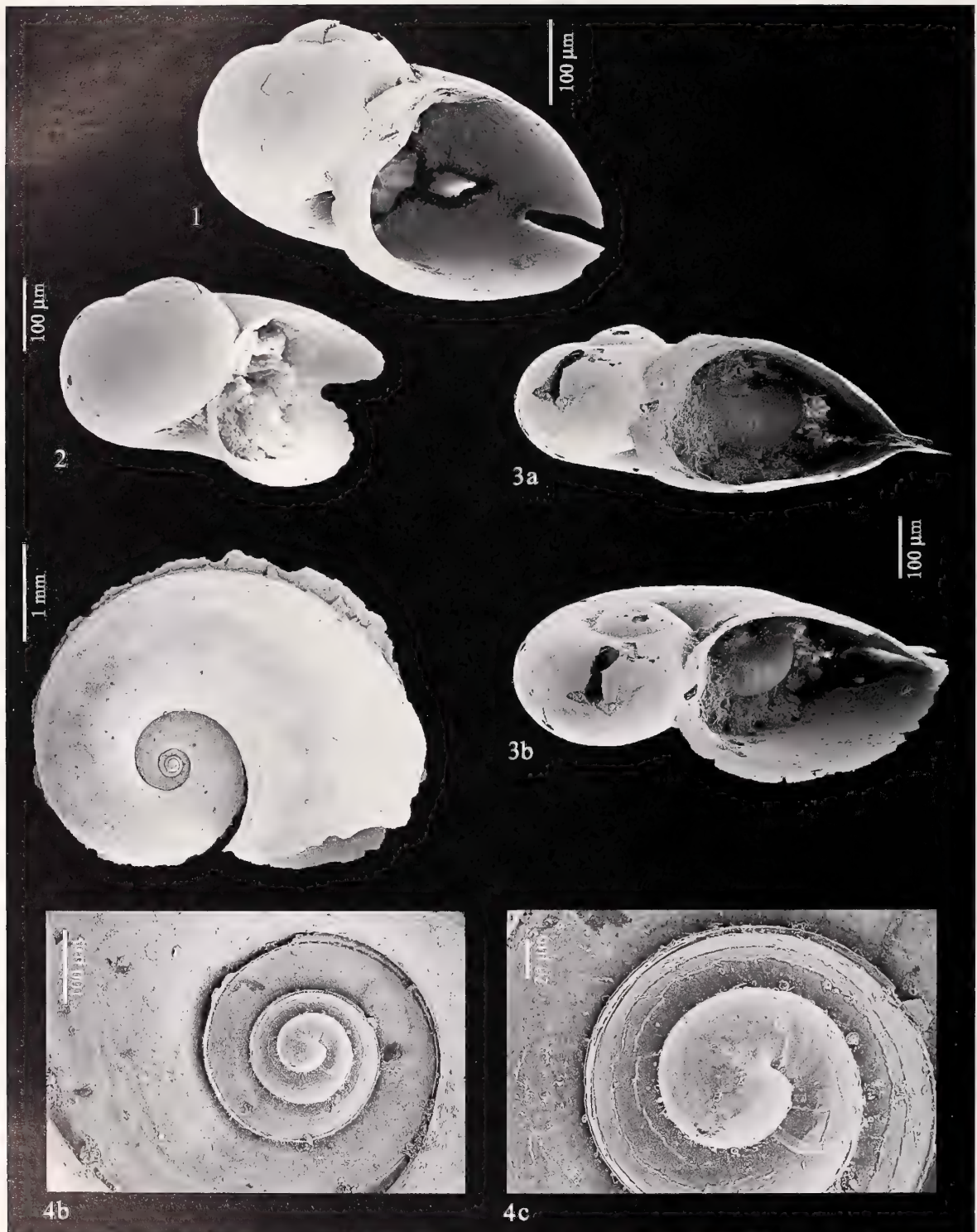


Plate 7. SEM-images of *Atlanta oligogyra* Tesch, 1906 (Figures 1–3, Red Sea, sample 11, RGM 540.380–540.382) and *A. plana* Richter, 1972 (Figure 4, Red Sea, sample 9, RGM 540.383). Figures 1–2: protoconchs, apertural views; Figure 3a: semi-adult specimen, apertural view; Figure 3b: idem, oblique apertural/apical view; Fig. 4a: adult specimen, apical view; Figure 4b: idem, protoconch enlarged; Figure 4c: idem, nucleus and first whorl enlarged.



Plate 8. SEM-images of *Atlanta plana* Richter, 1972 (Figure 1, Red Sea, sample 11, RGM 540.384; Figures 2–4, Red Sea, sample 13, RGM 540.385–540.387). Figure 1a: adult specimen, apertural view; Figure 1b: idem, oblique apertural/apical view; Figure 2a: protoconch, apertural view; Figure 2b: micro-ornament of nucleus; Figure 3a: protoconch, apertural view; Figure 3b: micro-ornament of nucleus; Figure 4: protoconch, apertural view.

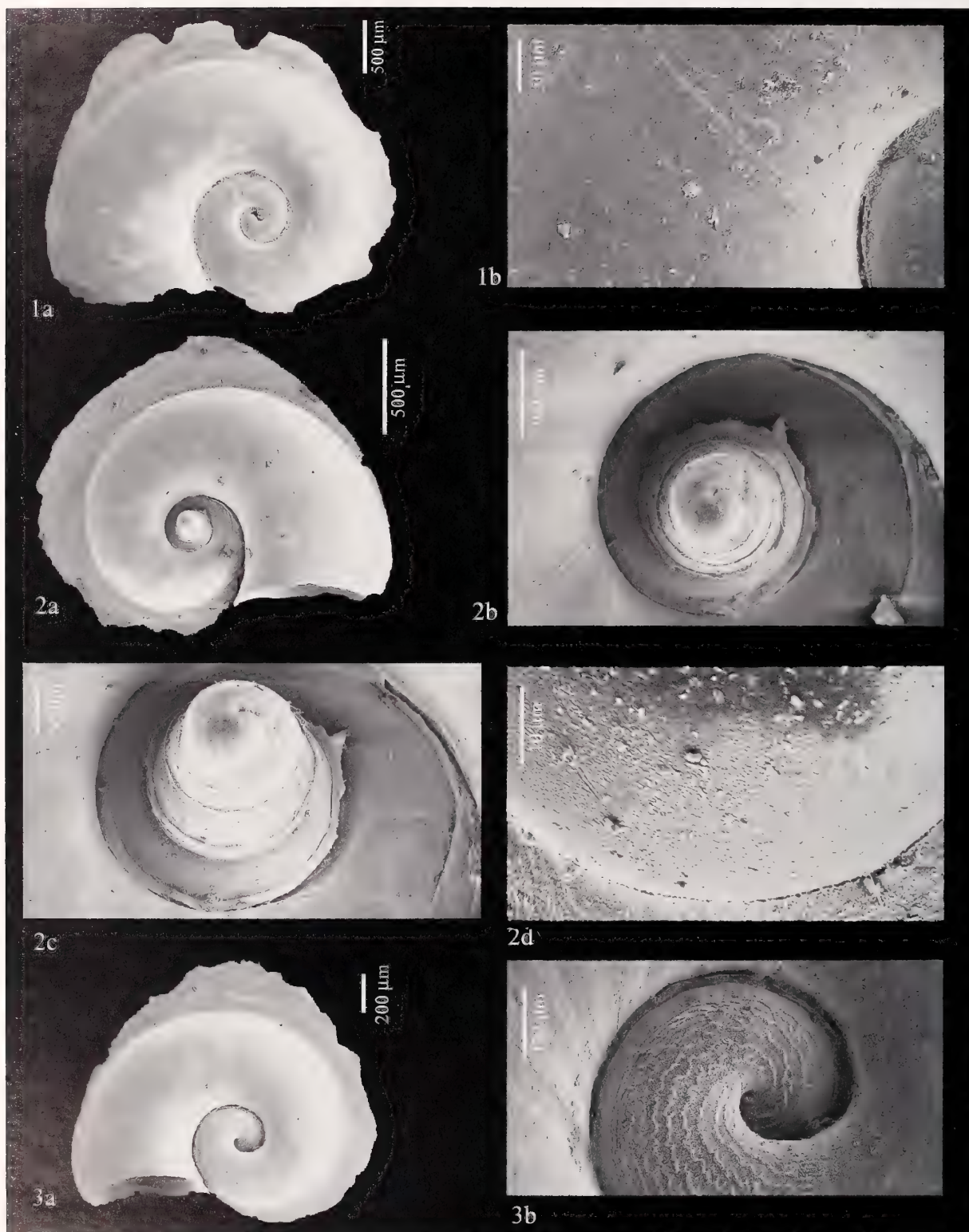


Plate 9. SEM-images of *Atlanta plana* Richter, 1972 (Figure 1, Red Sea, sample 13, RGM 540.388) and *A. turriculata* d'Orbigny, 1836 (Figures 2–3, Red Sea, sample 12, RGM 540.389–540.390). Figure 1a: adult specimen, umbilical view; Figure 1b: enlargement of Figure 1a; Figure 2a: adult specimen, apical view; Figure 2b: protoconch of same specimen; Figure 2c: oblique view of same; Figure 2d: micro-ornament of nucleus; Figure 3a: adult specimen, umbilical view; Figure 3b: enlargement of umbilical part of same specimen.

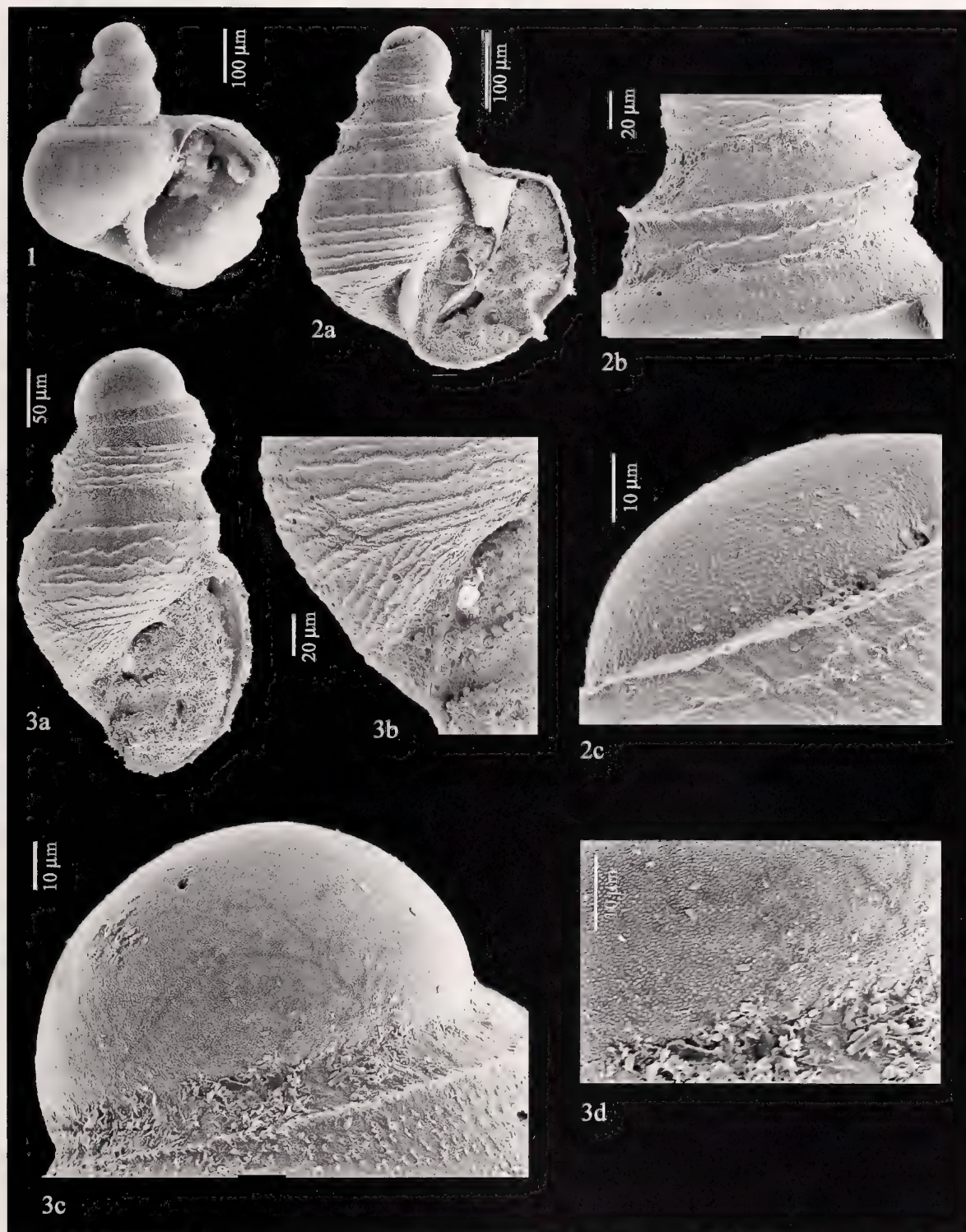


Plate 10. SEM-images of *Atlanta turriculata* d'Orbigny, 1836 (Figures 1, 2, Gulf of Aden, sample 15, RGM 540.391–540.392; Figure 3, Red Sea, sample 13, RGM 540.393). Figure 1: protoconch, apertural view; Figure 2a: protoconch, apertural view; Figure 2b: early whorl of same specimen; Figure 2c: micro-ornament of nucleus of same specimen; Figure 3a: protoconch, apertural view; Figure 3b: ornament on base of same specimen; Figure 3c: nucleus of same specimen; Figure 3d: micro-ornament of nucleus.

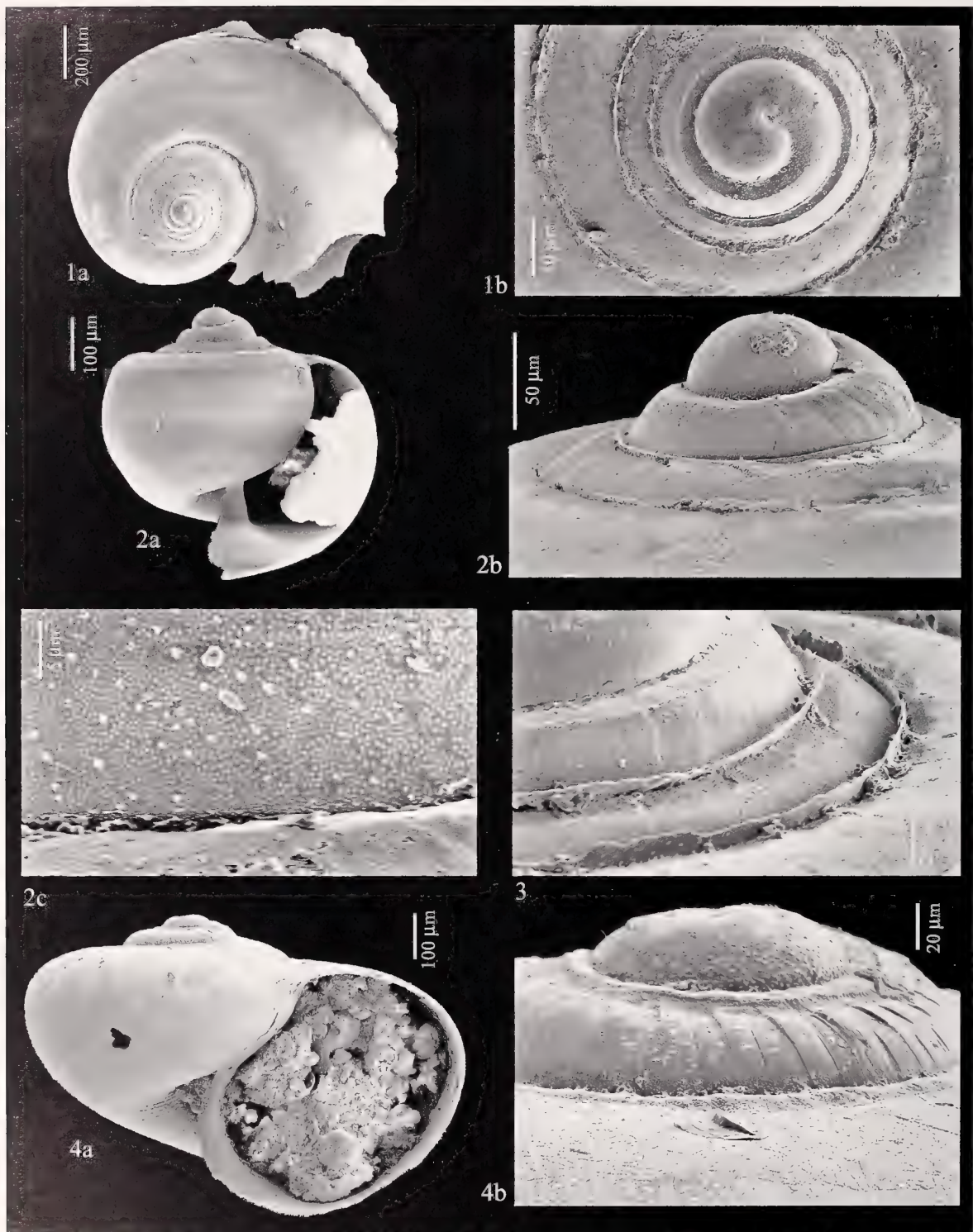


Plate 11. SEM-images of *Atlanta frontieri* Richter, 1993. (Figure 1, Red Sea, sample 11, RGM 540.394; Figures 2, 3, Gulf of Aden, sample 15, RGM 540.395–540.396) and *Carinariidae* sp. 1 (Figure 4, Gulf of Aden, sample 15, RGM 540.397). Figure 1a: juvenile specimen, apical view; Figure 1b: protoconch of same specimen, enlarged; Figure 2a: juvenile specimen, apertural view; Figure 2b: protoconch of same specimen, enlarged; Figure 2c: micro-ornament of nucleus of same specimen; Figure 3: ornament of early whorls; Figure 4a: protoconch, apertural view; Figure 4b: nucleus and first whorl of same specimen, enlarged.

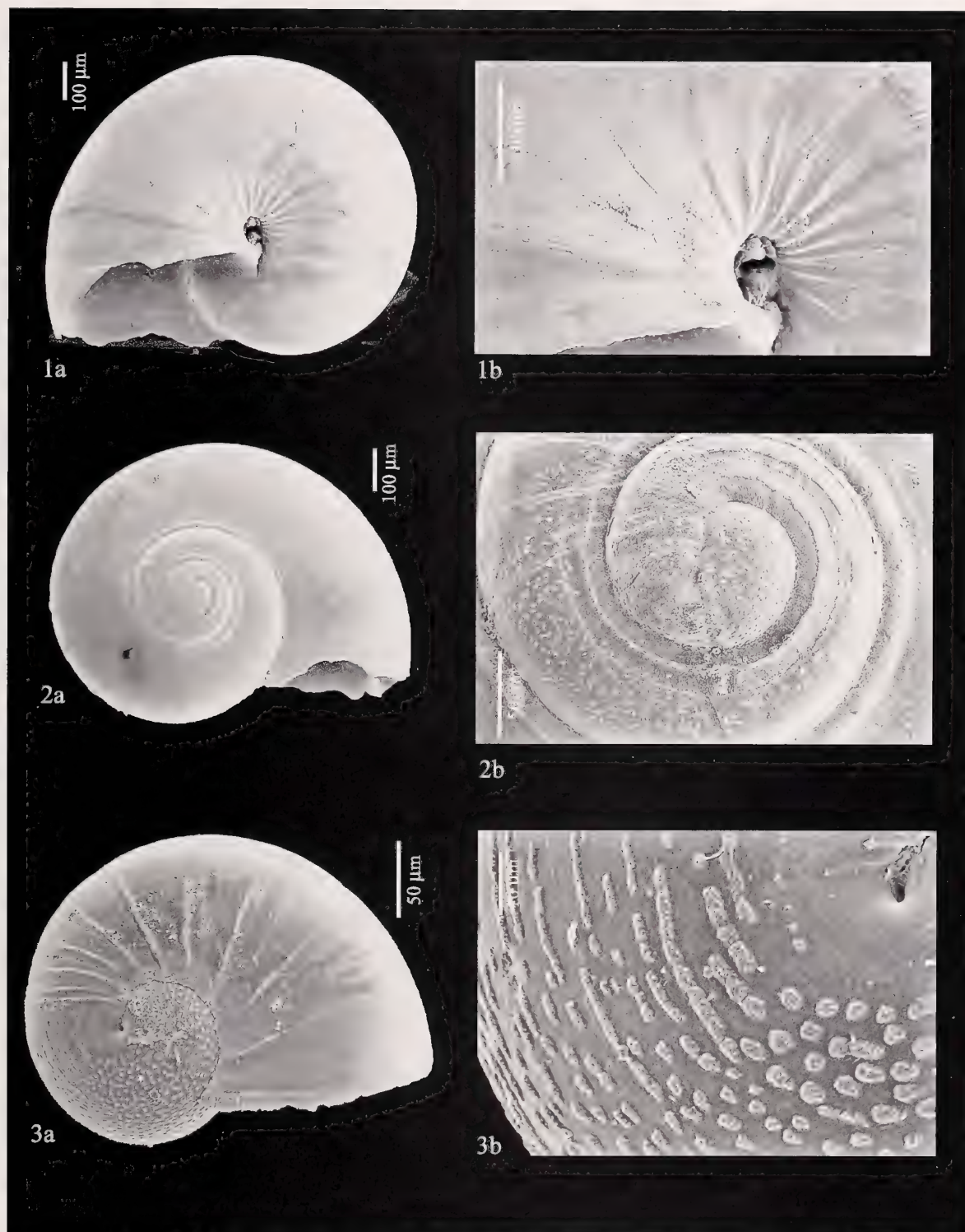


Plate 12. SEM-images of Carinariidae sp. 1 (Figures 1, 2, Gulf of Aden, sample 15, RGM 540.398–540.399) and Carinariidae sp. 2 (Figure 3, Gulf of Aden, sample 15, RGM 540.400). Figure 1a, protoconch, umbilical view; Figure 1b: umbilicus and base of same specimen, enlarged; Figure 2a: protoconch, apical view; Figure 2b: nucleus and first whorl of same specimen, enlarged; Figure 3a: protoconch, apical view; Figure 3b: micro-ornament of nucleus of same specimen.

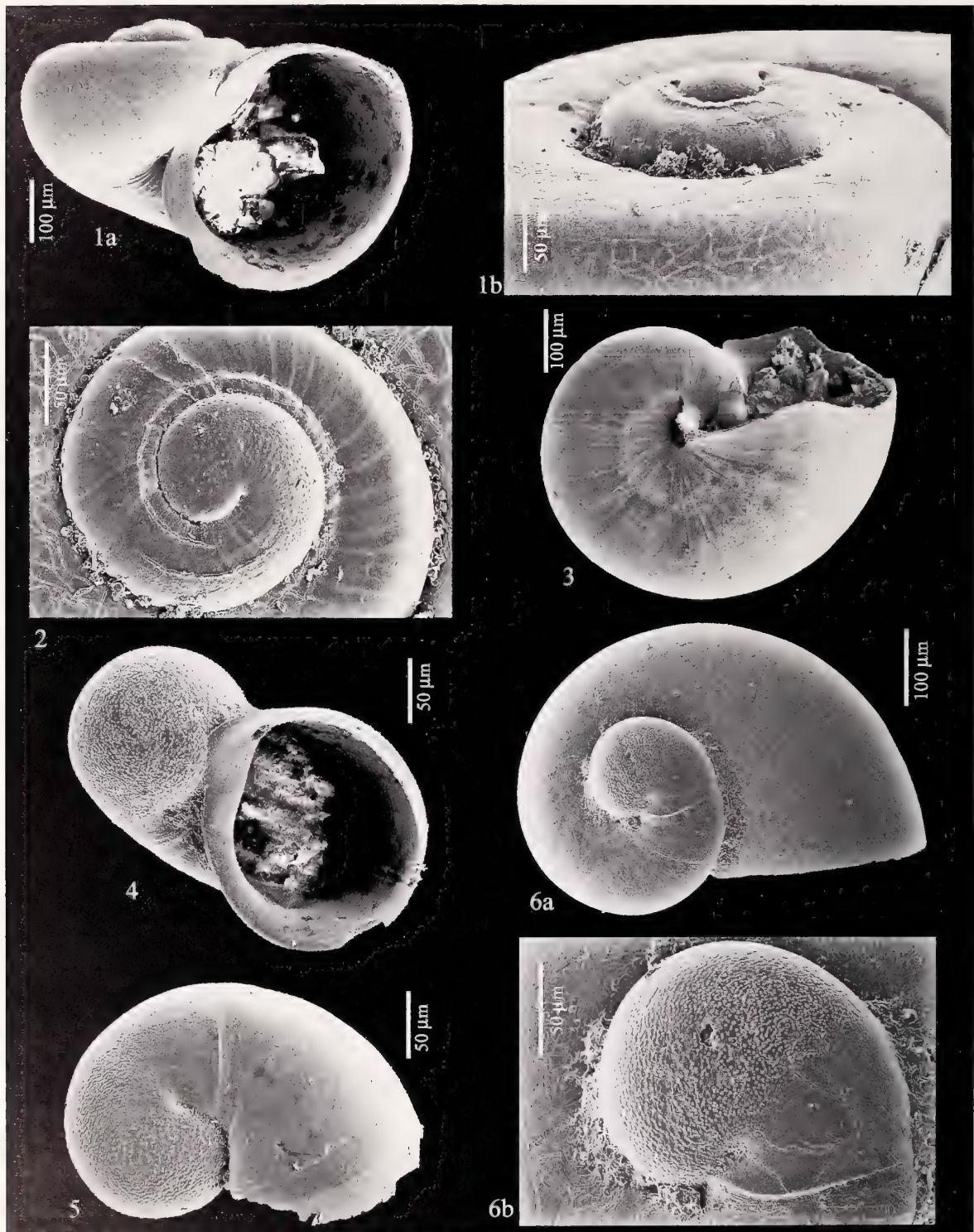


Plate 13. SEM-images of *Carinariidae* sp. 3 (Figures 1–3, Gulf of Aden, sample 15, RGM 540.401–540.403 and *Firoloida demarestia* Lesueur, 1817 (Figures 4–6, Red Sea, sample 7, RGM 540.404–540.405; sample 11, RGM 540.406). Figure 1a: protoconch, apertural view; Figure 1b: oblique apical view of same specimen; Figure 2: nucleus and first whorl, showing micro-ornament; Figure 3: protoconch, umbilical view; Figure 4: nucleus showing micro-ornament, and first half whorl, apertural view; Figure 5: nucleus showing micro-ornament, and first half whorl, apical view; Figure 6a: protoconch, apical view; Figure 6b: nucleus same specimen, showing micro-ornament.

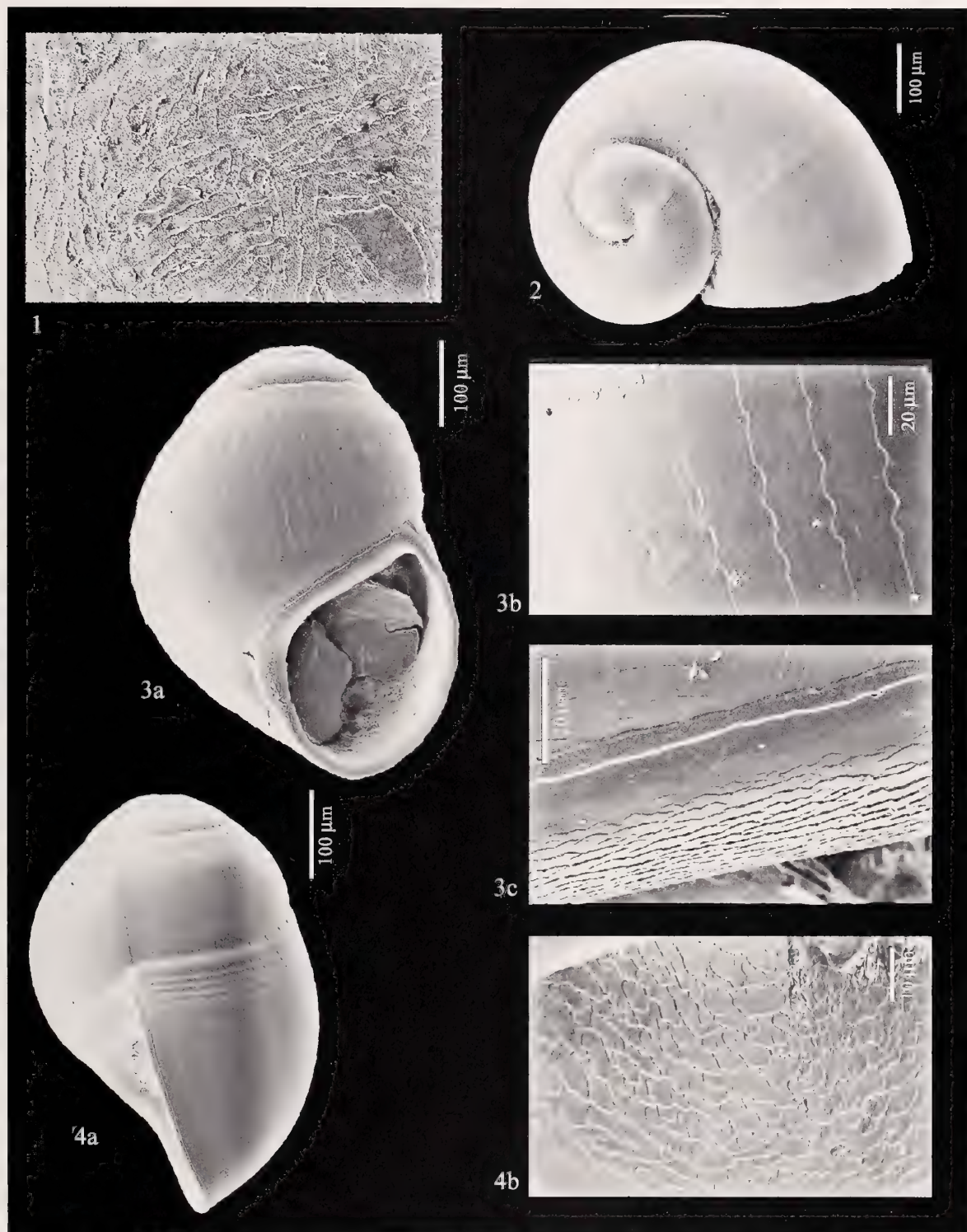


Plate 14. SEM-images of *Fioloida demarestia* Lesueur, 1817 (Figure 1, 2, Red Sea, sample 11, RGM 540.406–540.407) and *Janthina* sp. (Figures 3–4, Red Sea, sample 11, RGM 540.408–540.409). Figure 1: bio-erosion (?) on surface of protoconch illustrated Pl. 13, fig. 6; Figure 2: protoconch, apical view; Figure 3a: protoconch, apertural view; Figure 3b: radial ornament on bodywhorl of same specimen; Figure 3c: aragonite scales on palatal part of apertural margin of same specimen; Figure 4a: protoconch, lateral view; Figure 4b: aragonite scales on columellar callus of same specimen.



Plate 15. SEM-images of *Heliconoides inflata* (d'Orbigny, 1836) (Figures 1, 2, Red Sea, sample 12, RGM 540.410–540.411); *Limacina bulimoides* (d'Orbigny, 1836) (Figures 3–5, Red Sea, sample 7, RGM 540.412–540.413; sample 13, RGM 540.414) and *Limacina trochiformis* (d'Orbigny, 1836) (Figures 6–9, Red Sea, sample 4, RGM 540.415–540.416; sample 8, RGM 540.417; sample 14, RGM 540.418). Figure 1: adult specimen, lateral view; Figure 2: adult specimen, apical view; Figure 3: adult specimen, apertural view; Figure 4: adult specimen, lateral view; Figure 5a: juvenile specimen, apertural view; Figure 5b: apex of same specimen, showing micro-ornament; Figure 6a: adult specimen, apertural view; Figure 6b: micro-ornament at beginning of body whorl of same specimen; Figure 7: adult specimen, lateral view; Figures 8, 9: juvenile specimens, apertural views.

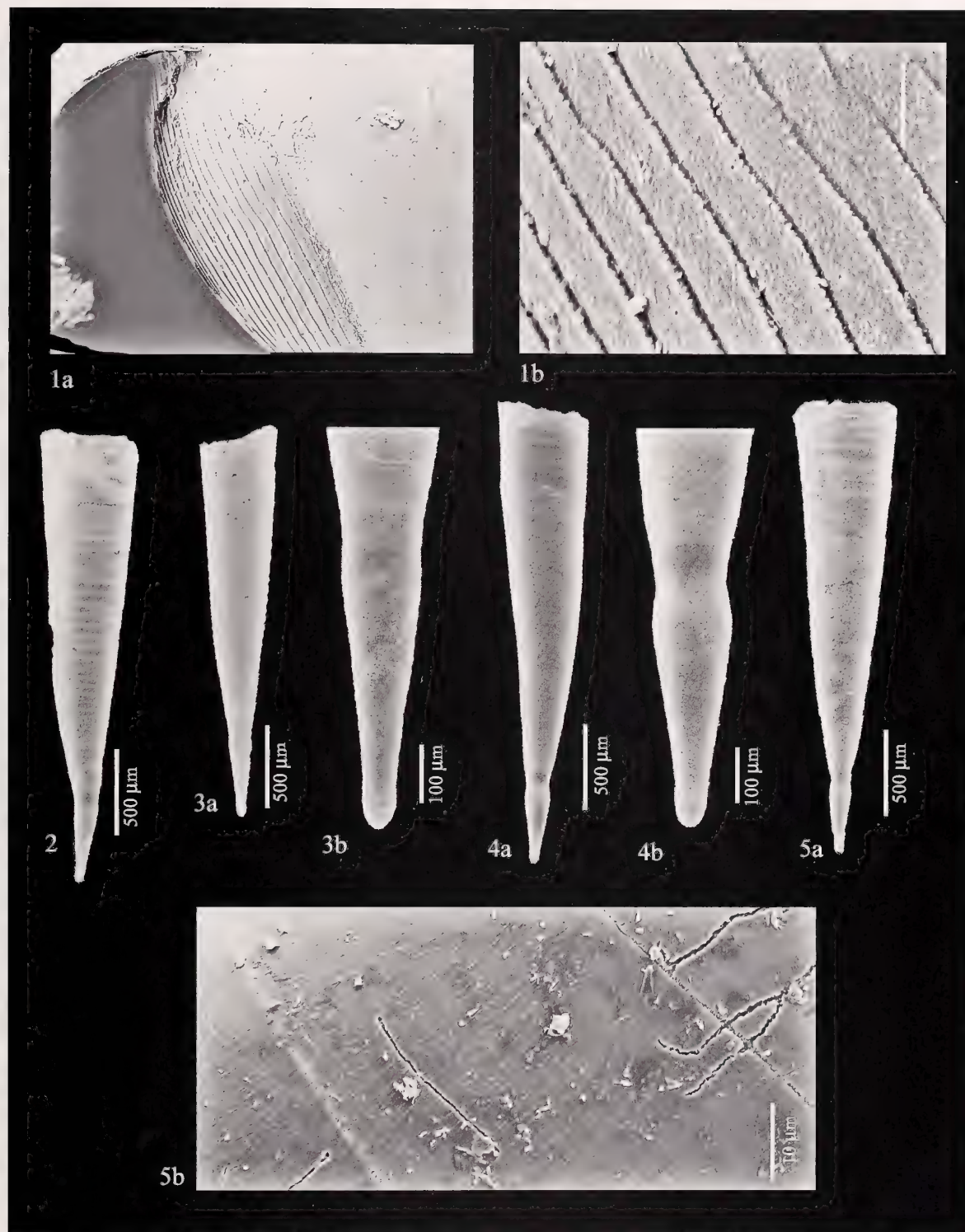


Plate 16. SEM-images of *Limacina trochiformis* (d'Orbigny 1836) (Figure 1, Red Sea, sample 14, RGM 540.418), *Creseis chierchiae* (Boas, 1886) (Figure 2, 3, Red Sea, sample 7, RGM 540.419; sample 11, RGM 540.420) and *Creseis chierchiae* (Boas, 1886) forma *constricta* Chen & Bè, 1964 (Figure 4, Gulf of Aden, sample 15, RGM 540.421; Figure 5, Red Sea, sample 7, RGM 540.422). Figure 1a: palatal side of aperture, showing radial ridges; Figure 1b: same specimen, radial ridges enlarged; Figure 2: adult specimen, ventral view; Figure 3a: adult specimen, lateral view; Figure 3b: same specimen, protoconch enlarged; Figure 4a: adult specimen, lateral view; Figure 4b: same specimen, protoconch enlarged; Figure 5a: adult specimen, dorsal view; Figure 5b: micro-ornament of same specimen.



Plate 17. SEM-images of *Creseis clava* (Rang, 1828) (Figures 1, 2, Red Sea, sample 11, RGM 540.423–540.424); *Creseis conica* Eschscholtz, 1829 (Figures 3, 4, Red Sea, sample 13, RGM 540.425–540.426) and *Creseis virgula* (Rang, 1828) (Figures 5, 6, Red Sea, sample 12, RGM 540.427–540.428). Figure 1: semi-adult specimen; Figure 2a: adult specimen; Figure 2b: protoconch of same specimen, enlarged; Figure 3a: adult specimen, curved form; Figure 3b: protoconch of same specimen, enlarged; Figure 4a: adult specimen, straight form; Figure 4b: protoconch of same specimen, enlarged; Figure 5a: adult specimen, lateral view; Figure 5b: protoconch of same specimen, enlarged; Figure 6a: adult specimen, slightly flexuous form; Figure 6b: protoconch of same specimen, enlarged.

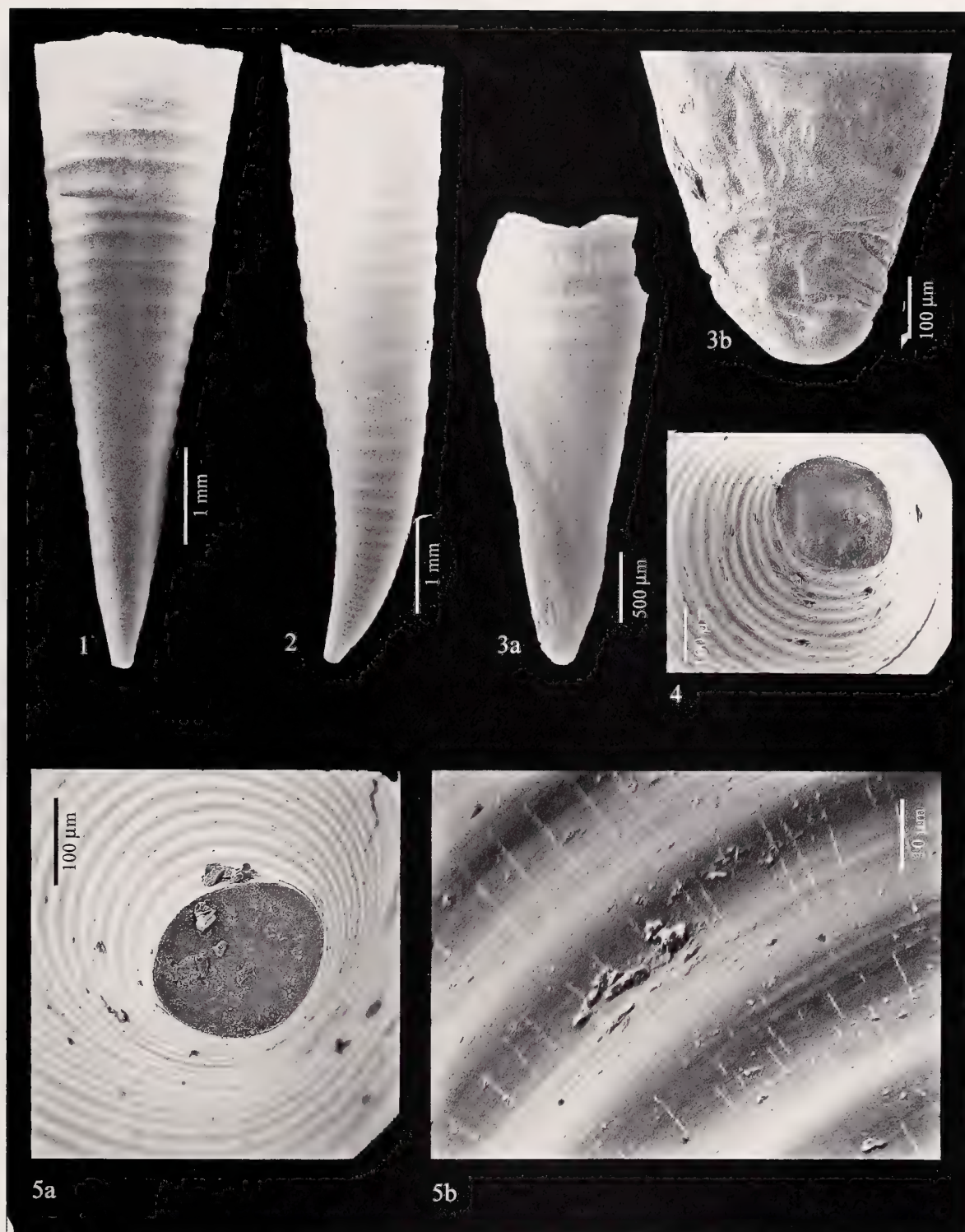


Plate 18. SEM-images of *Hyalocyclus striata* (Rang, 1828) (Figures 1, 2, Red Sea, sample 7, RGM 540.429–540.430; Figures 3, 4, Gulf of Aden, sample 15, RGM 540.431–540.432; Figure 5, Red Sea, sample 7, RGM 540.433). Figure 1: adult specimen, dorsal view; Figure 2: adult specimen, lateral view; Figure 3a: specimen with wrinkled apical portion; Figure 3b: apical portion, enlarged; Figure 4: apical view, showing septum; Figure 5a: apical portion, showing septum; Figure 5b: micro-ornament between annulations.

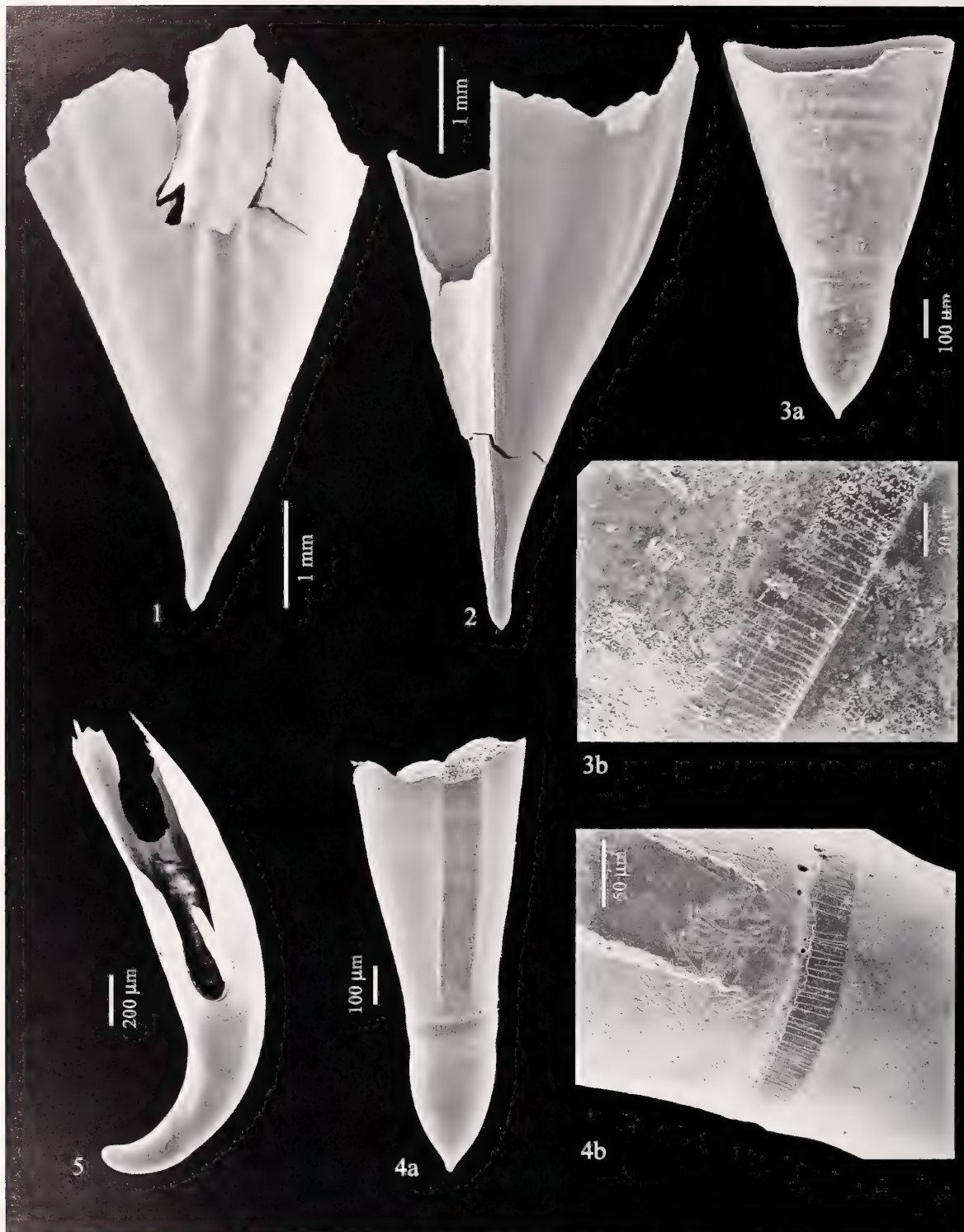


Plate 19. SEM-images of *Clio* (*Clio*) *convexa cyphosa* Rampal, 2002 (Figures 1, 2, Red Sea, sample 12, RGM 540.434–540.435; Figures 3, 4, Gulf of Aden, sample 15, RGM 540.436–540.437) and Cavoliniidae sp. (Figure 5, Red Sea, sample 11, RGM 540.438). Figure 1: adult specimen, dorsal view; Figure 2: adult specimen, left lateral view; Figure 3a: juvenile specimen, ventral view; Figure 3b: same specimen, showing radial micro-ornament on the boundary of protoconch and teleoconch; Figure 4a: juvenile specimen, right lateral view; Figure 4b: same specimen, showing micro-ornament on the boundary of protoconch and teleoconch; Figure 5: juvenile specimen, right lateral view.



Plate 20. Photographs of *Cavolinia uncinata* (Rang, 1829) (Figure 1, Red Sea, sample 6, RGM 540.439), *Diacavolinia angulata* (Souleyet, 1852) (Figure 2, Gulf of Aden, sample 15, RGM 539.947) and *Diacavolinia flexipes* van der Spoel, Bleeker & Kobayashi, 1993 (Figure 3, Red Sea, sample 12, RGM 540.440). Adult specimens, a: dorsal view, b: left lateral view, c: ventral view.

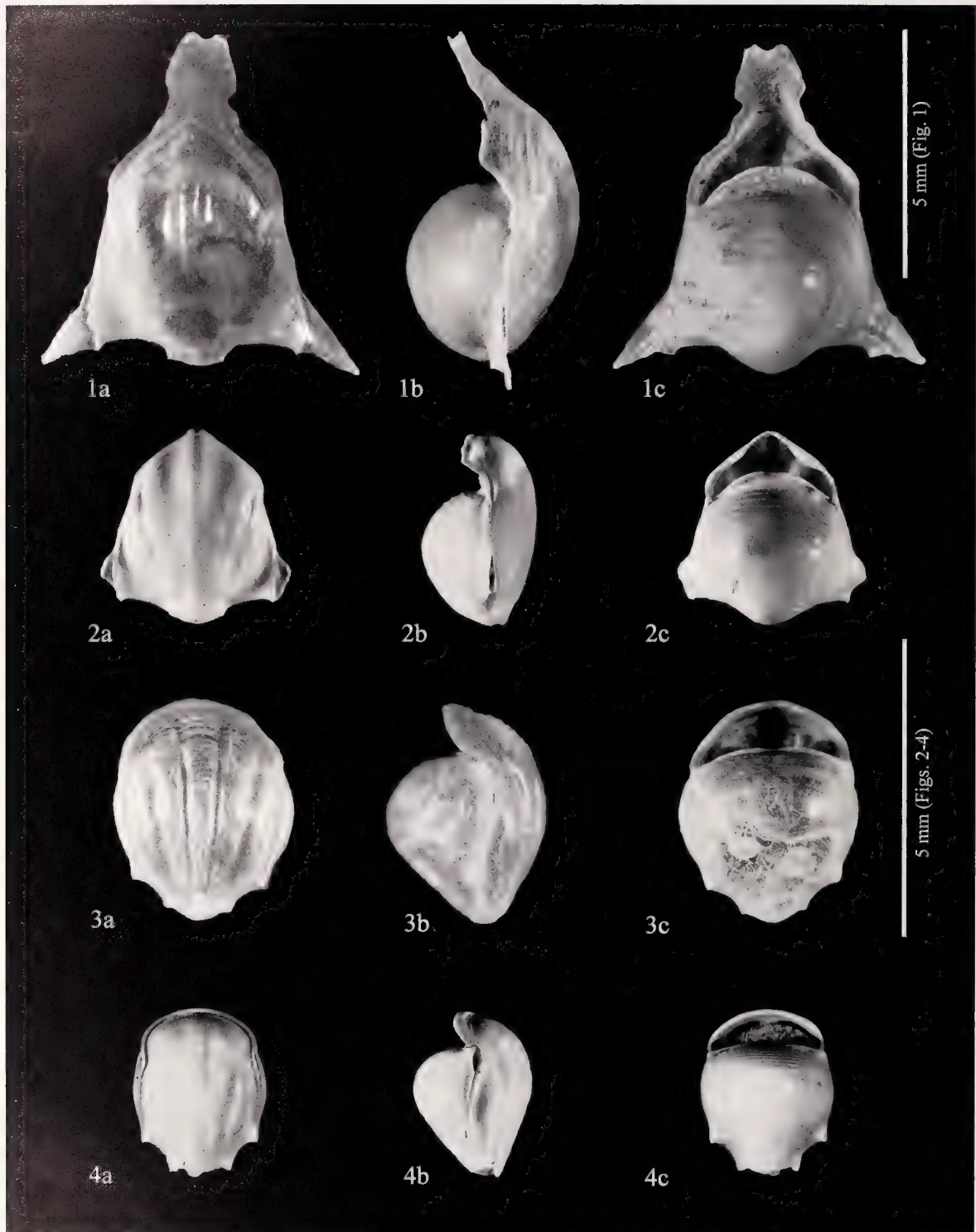


Plate 21. Photographs of *Diacavolinia longirostris* (de Blainville, 1821) (Figure 1, Gulf of Aden, sample 15, RGM 540.441); *Diacavolinia* sp. (Figure 2, Gulf of Aden, sample 15, RGM 540.442); *Diacria erythra* van der Spoel, 1971 (Figure 3, Red Sea, sample 12, RGM 540.443); and *Diacria quadridentata* (de Blainville, 1821) (Figure 4, Gulf of Aden, sample 15, RGM 540.444). Adult specimens, a: dorsal view, b: left lateral view, c: ventral view.



Plate 22. SEM-images of Cavoliniidae (Figure 1, Red Sea, sample 11, RGM 540.445), *Diacria erythra* van der Spoel, 1971 (Figures 2, 3, Red Sea, Sample 7, RGM 540.446–540.447), *Cymbulia* sp. 1 (Figures 4–6, Red Sea, sample 13, RGM 540.448–540.450) and *Cymbulia* sp. 2 (Figures 7–9, Red Sea, sample 7, RGM 540.451–540.453). Figure 1: juvenile specimen, dorsal view; Figure 2: juvenile specimen, protoconch broken, dorsal view; Figure 3a: juvenile specimen with protoconch, dorsal view; Figure 3b: same specimen, protoconch enlarged; Figure 4: larval shell, apical view; Figure 5: larval shell, apertural view; Figure 6: larval shell, umbilical view; Figure 7: larval shell, apertural view; Figure 8: larval shell, apical view; Figure 9: larval shell, umbilical view.

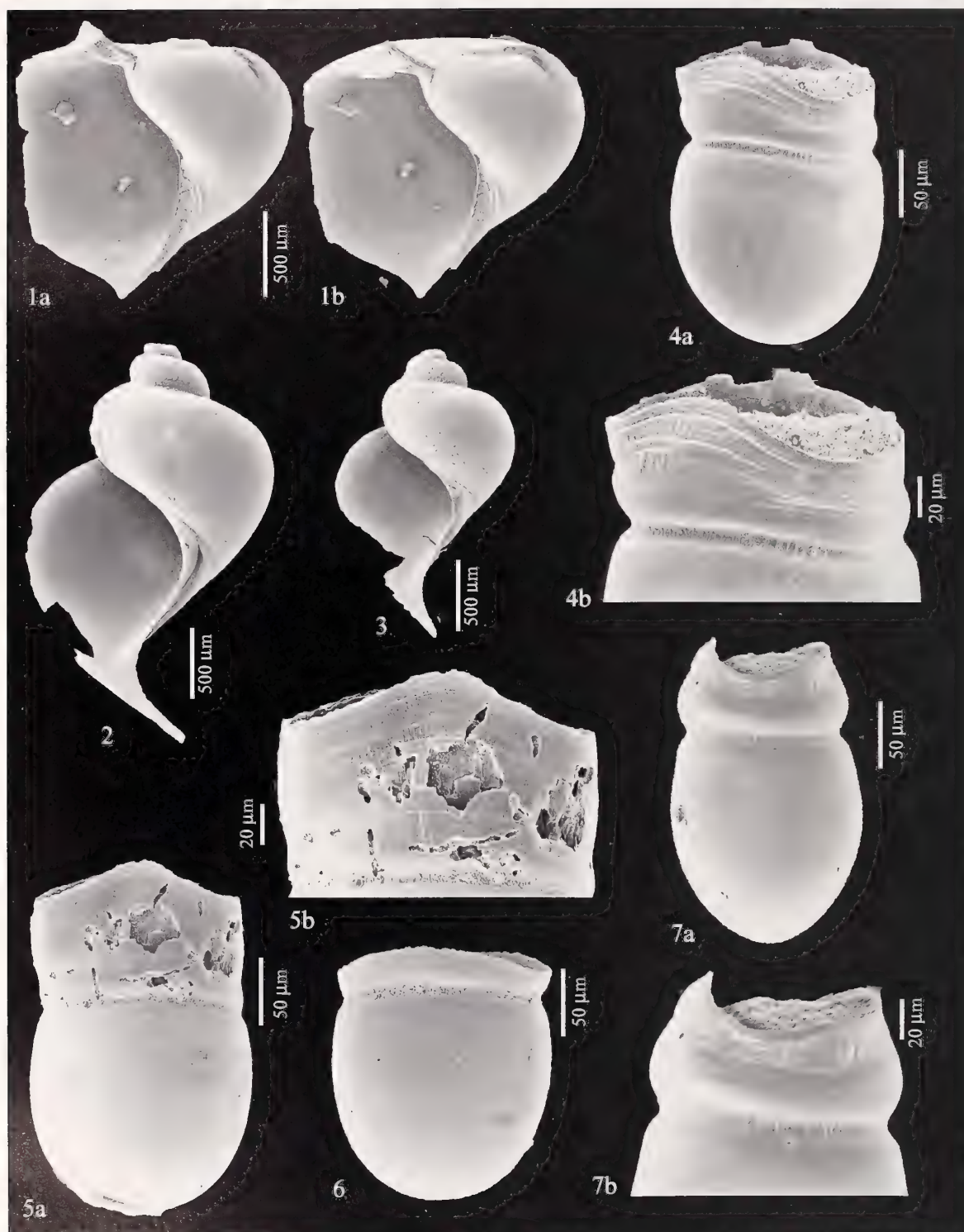


Plate 23. SEM-images of *Peracelis moluccensis* Tesch, 1903 (Figure 1, Gulf of Aden, sample 15, RGM 540.454), *Peracelis reticulata* (d'Orbigny, 1836) (Figure 2, 3, Red Sea, sample 12, RGM 540.455; sample 7, RGM 540.456) and *Gymnosomata* sp. 1 (Figures 4, 6 and 7, Red Sea, sample 13, RGM 540.457–540.459; Figure 5, Gulf of Aden, sample 15, RGM 540.460). Figure 1a: juvenile specimen, apertural view; Figure 1b: same specimen, oblique apertural/apical view; Figure 2: adult specimen, apertural view; Figure 3: adult specimen with remnants of reticulate cuticulum, apertural view; Figure 4a: larval shell, oblique frontal/lateral view; Figure 4b: same specimen, apertural part enlarged; Figure 5a: larval shell, frontal view; Figure 5b: same specimen, apertural part enlarged; Figure 6: larval shell, with early teleoconch (?) not developed; Figure 7a: larval shell, lateral view; Figure 7b: same specimen, apertural part enlarged.

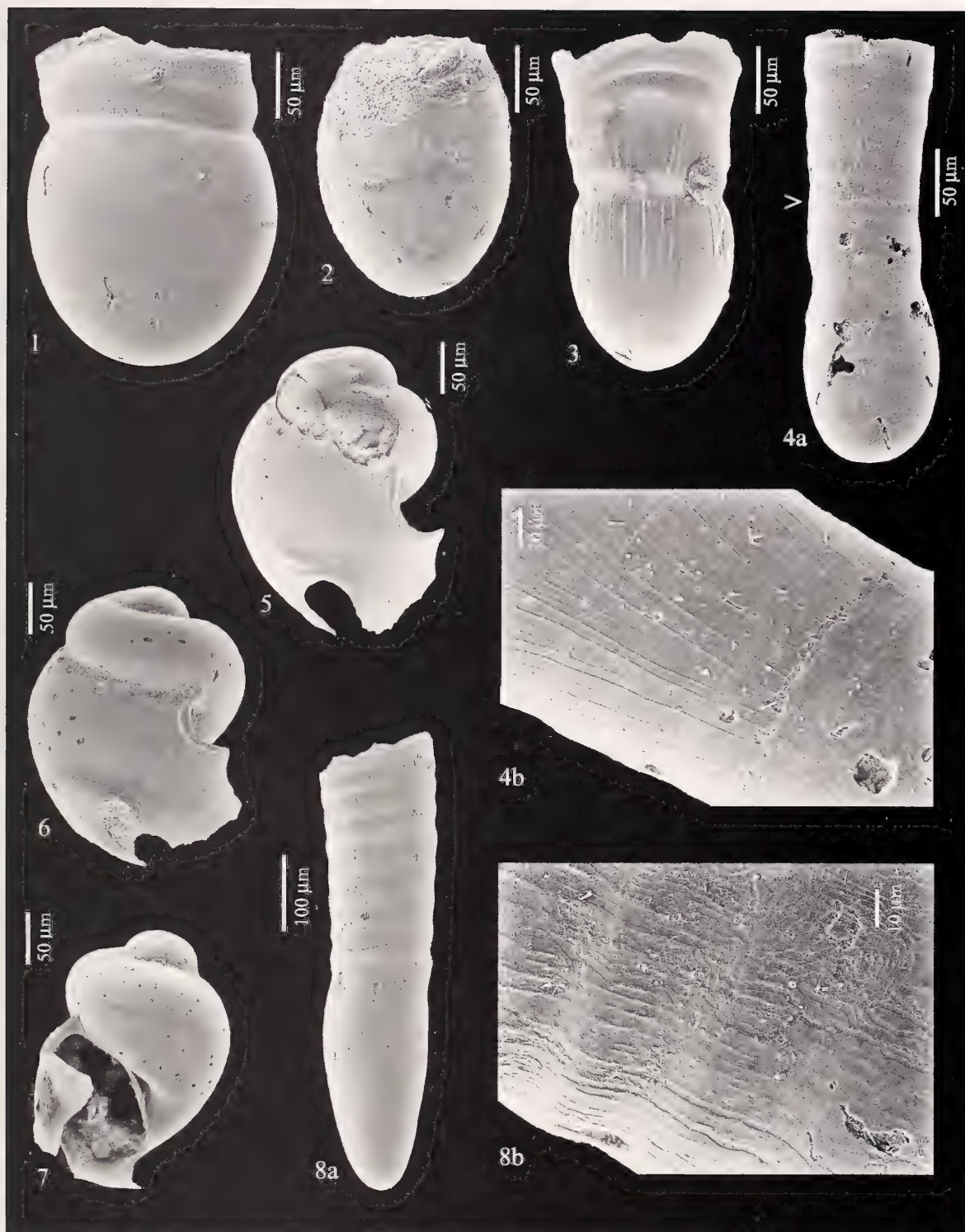


Plate 24. SEM-images of *Gymnosomata* sp. 1 (Figure 1, Red Sea, sample 7, RGM 539.895), *Gymnosomata* sp. 2 (Figure 2, Red Sea, sample 7, RGM 540.461); *Gymnosomata* sp. 3 (Figure 3, Red Sea, sample 13, RGM 539.897), *Gymnosomata* sp. 4 (Figure 4, Red Sea, sample 13, RGM 539.992), veliger larva of unknown gastropod (Figures 5–6, Red Sea, sample 7; RGM 540.462–540.463; Figure 7, Red Sea, sample 13, RGM 540.464) and 'beaked larva' *sensu* van der Spoel & Newman, 1990 (Figure 8, Red Sea, sample 7, RGM 539.898). Figure 1: larval shell, frontal view; Figure 2: larval shell, damaged, frontal view; Figure 3: larval shell, frontal view; Figure 4a: larval shell, frontal view (> indicates the boundary between protoconch-2 and early teleoconch); Figure 4b: same specimen, micro-ornament of longitudinal ridges on early teleoconch; Figures 5, 6: larval shell, lateral views; Figure 7: larval shell, apertural view; Figure 8a: protoconch and early shell parts; Figure 8b: micro-ornament on early shell part beyond protoconch.

as a reinforcement. These structures resemble some veliger larvae of benthic gastropods, but none of the many available specimens demonstrates a further development beyond the apertural protoconch margin. The sinistral coiling of the shells suggests an opisthobranch species. Very similar, if not identical, specimens in phosphoritic internal mould preservation are available from the Miocene of Malta (RGM collections).

'Beaked larva' *sensu* van der Spoel & Newman, 1990

Pl. 24, fig. 8a, b

1990 Beaked larva—van der Spoel & Newman, p. 207, fig. 5 (and references therein).

Discussion—A single, incomplete specimen was collected from sample 7. Although it shows resemblances with some of the Gymnosomata discussed above it seems to represent a specimen of what was called 'beaked larva' by van der Spoel & Newman (1990). The shape of the elongately oval initial shell part and the annulations on the younger shell part agree completely. This latter part also bears a somewhat irregular longitudinal micro-ornament (Pl. 24, fig. 8b). The apertural shell parts with the structures, described by van der Spoel & Newman, are missing in this specimen.

RESULTS

The present study leads to conclusions about the actual holoplanktonic mollusc stock in the Red Sea. As all material is from bottom samples no living specimens were seen. In practically all cases, however, the samples contain fresh specimens the age of which, as demonstrated by von Rützen-Kositzkau (1999: 49) is no more than maximally ~6 kA. It is assumed that all species found in the bottom samples do occur alive at the present day.

Only epi- and mesopelagic species were found. Bathypelagic species are absent. Weikert (1982, tab. 3) found a strong reduction of pteropod abundances below 750 m sea depth, and related this phenomenon to high temperature and salinity, together with strongly reduced oxygen contents and a lack of food. Weikert (1987) found the lowest oxygen contents between 200 and 640 m, increasing again below 750 m.

A clear distinction can be made in a first group of species occurring all over the Red Sea, a second group only occurring in the southeastern part, and a third group occurring in the Gulf of Aden, but absent in the Red Sea proper. These groups are specified in Table 3.

All pteropod species recorded from the Gulf of Aqaba and the northernmost Red Sea by Almogi-Labin (1984, p. 495) occur also in group 1 (Table 3). Some species of group 1, however, according to her data have not reached the Gulf of Aqaba, *viz.* *Creseis*

chierchiae f. *constricta* and *Hyalocylis striata*, which is acknowledged by my results (Table 2). The same is true for several further species, as indicated in Table 3. Earlier records (Almogi-Labin & Reiss, 1977) of '*Cuvierina columnella urceolaris*' and *Clio polita* are corrected by Almogi-Labin (1984) as respectively 'a gastropod' (but in reality is a siphonodentalioid scaphopod) and 'a gymnosomate pteropod' (most probably identical with *Gymnosomata* sp. 1 in the present paper).

Species in group 2 obviously do not tolerate the stress of northward increasing salinity. High temperature cannot be a factor here, as it decreases in northern direction. The same tendency is visible in some species of group 1 that, although present all over the Red Sea, show distinctly decreasing numbers of specimens per sample in northwestern direction, *viz.* *Atlanta turriculata*, *Creseis hierchiae* f. *constricta*, *Hyalocylis striata* and *Diacavolinia flexipes*. All specifically identified Group 3 species, absent in the Red Sea, but found in the Gulf of Aden sample, have a wider distribution in the Indian Ocean, but most of them occur in low numbers, indicating that already in the Gulf of Aden the environment is less favourable than in more open oceanic surroundings.

This latter statement is also indicated by species present in the open Indian Ocean (albeit sometimes rare), but not found in the Gulf of Aden sample, such as *Atlanta gaudichaudi* Souleyet, 1852, *A. gibbosa* Souleyet, 1852, *A. inflata* Souleyet, 1852, *A. meteori* Richter, 1972, *Protatlanta souleyeti* (Smith, 1888), several Carinariidae (which may be represented, however, by unidentified larval shells, see Carinariidae spp. 1–3, above) and Pterotracheidae species, *Cuvierina urceolaris* (Mörch, 1850), *Cavolinia globulosa* (Gray, 1850), *C. inflexa* (Lesueur, 1813) and *Peraclis apicifulva* (Meisenheimer, 1906) (most data from Richter, 1974, 1979, 1993). Van der Spoel's (1976) distribution maps additionally indicate the occurrence of the following gymnosomatous species in the NW Indian Ocean: *Pneumodermopsis paucidens* (Boas, 1886), *Pneumoderma mediterraneum* (van Beneden, 1838), *Pruvotella pellucida* (Quoy & Gaimard, 1832), *Thliptodon diaphanus* (Meisenheimer, 1902), *Cliopsis krohni* Troschel, 1854, and *Paraclione longicaudata* (Souleyet, 1852). The specimens here indicated as *Gymnosomata* spp. potentially can belong to these taxa.

C. inflexa was recorded from the Gulf of Aqaba by Yaron (1977, p. 75) and from the Red Sea by Weikert (1982, p. 136). As that species is absent from all samples studied here I consider these records doubtful, their identification has to be checked.

A single specimen of '*Cuvierina columnella* (Rang, 1827)' was recorded from the Red Sea by Bandel & Hemleben (1995, p. 235, fig. 6E). Most probably this was a 'lost' specimen of *C. urceolaris* (Mörch, 1850), compare

Table 3

Holoplanktonic mollusc species found in the present study distributed all over the Red Sea (group 1, * = also Gulf of Aqaba), only in the southeastern part of the Red Sea (group 2) and absent from the Red Sea, but present in the Gulf of Aden (group 3).

Group 1	Group 2	Group 3
<i>Atlanta fusca</i>	<i>Atlanta echinogyra</i>	<i>Oxygyrus keraudreni</i>
<i>Atlanta helicinoides</i>	<i>Atlanta frontieri</i>	Carinariidae sp. 2
* <i>Atlanta inclinata</i>	<i>Atlanta lesueuri</i>	<i>Styliola subula</i>
<i>Atlanta oligogyra</i>	<i>Atlanta plana</i>	<i>Clio pyramidata</i> f. <i>lanceolata</i>
<i>Atlanta turriculata</i>	Carinariidae sp. 1	<i>Diacavolinia angulata</i>
* <i>Heliconoides inflata</i>	Carinariidae sp. 3	<i>Diacavolinia longirostris</i>
<i>Limacina bulimoides</i>	<i>Firoloida demarestia</i>	<i>Diacavolinia</i> sp.
* <i>Limacina trochiformis</i>	<i>Janthina</i> sp.	<i>Diacria quadridentata</i>
<i>Creseis chierchiaie</i> f. <i>constricta</i>	<i>Creseis chierchiaie</i>	<i>Diacria trispinosa</i>
* <i>Creseis clava</i>	<i>Creseis conica</i>	<i>Peraclis moluccensis</i>
* <i>Creseis virgula</i>	<i>Clio cuspidata</i> ?	
<i>Hyalocyclus striata</i>	<i>Cymbulia</i> sp. 2	
* <i>Clio convexa cyphosa</i>	Gymnosomata spp. 1–4	
* <i>Cavolinia uncinata</i>		
* <i>Diacavolinia flexipes</i>		
* <i>Diacria erythra</i>		
<i>Cymbulia</i> sp. 1		
<i>Peraclis reticulata</i>		

the distribution map in Janssen (2005, fig. 35). Their illustration only shows the apical shell part with septum.

Dekker & Orlin (2000, p. 24) listed 5 species of Atlantidae for the Red Sea, of which, however, *Atlanta peroni* was not encountered during the present study. *A. brunnea* Gray, 1850, mentioned by these authors, is a synonym of *A. fusca*. Additionally, they refer (p. 25) to 5 species of Janthinidae (see above for a discussion) and (p. 35) to 13 taxa of Thecosomata, of which, however, the species *Cavolinia inflexa*, *C. tridentata* (Niebuhr, 1775), *Clio pyramidata* Linné, 1767 and *Styliola subula* do not belong to the actual Red Sea fauna. *Desmopterus papilio* Chun, 1889 and one gymnosomatous species, *Pneumoderma peronii* (Lamarck, 1819), mentioned for the Red Sea by these authors, were not recognised in the present sample material, but may have been based on live specimens from plankton hauls. *C. tridentata* was recorded from the Gulf of Aqaba by Barash & Zenziper (1994, p. 58), but not illustrated. I consider that a very doubtful record.

Professor Klaus Bandel (Geologisches Institut, Universität Hamburg, Germany) (in litt., 2006) noted the common presence of the (more or less) holoplanktonic nudibranch *Glaucus atlanticus* Forster, 1777 (superfamily Aeolidioidea Gray, 1827, family Glaucidae Gray, 1827) in plankton hauls of the southern Red Sea, but did not include this record in Bandel et al. (1997), as their reproduction could not be studied.

FOSSIL OCCURRENCES

Several species not found during this study in the Red Sea were recorded as fossils from that area in literature. Chen (1969) distinguished four layers in late-pleistocene and holocene hot brine sediments (covering c. 70 kA) containing pteropods, of which only some are mentioned, all of these also occurring in the present samples. Berggren (1969) summarised his results, and compared them to other disciplines.

Herman (1971, tab. 35.8) found, among other species, *Cavolinia inflexa* from northern Red Sea postglacial cores and *Diacria trispinosa* in cores from several last glacial stages. In her tab. 35.9 she referred to other species, viz. *Cavolinia globulosa* and *Clio pyramidata*. The actual presence of the former of these two in the Red Sea was acknowledged only by Rampal (1985; see above).

Almogi-Labin (1982) found *C. inflexa*, *D. trispinosa*, *Styliola subula* and a *Peraclis* species different from *P. reticulata* in the Pleistocene marine isotope stage 5. *Hyalocyclus striata* is in that paper also recorded from the Gulf of Aqaba as a holocene/pleistocene fossil. Similar data on holocene/pleistocene fossils are given by Almogi-Labin (1986) and Almogi-Labin et al. (1998). A specifically unidentified *Peraclis* species, occurring next to *P. reticulata*, was also recorded by Rampal (1985).

Ivanova (1985) studied Late Quaternary biostratigraphy and paleotemperatures in cores from the Red

Sea and Gulf of Aden. From her stratigraphic interval-I in the Red Sea, comprising the last 11 kA, this author recorded the species *Styliola subula*, *Cavolinia inflexa* and *Diacria trispinosa*, species presently no more occurring in the Red Sea fauna. For the Gulf of Aden she recorded an additional species, not found in my Gulf of Aden sample, viz. *Limacina lesueuri* (d'Orbigny, 1836). *Gymnosomata* sp. 1 is recorded by her from almost all samples (intervals I–V, comprising c. 100kA), but misidentified as *Clio polita* (Pelseneer). It is only absent in her interval-I sample from the Gulf of Aden. *Clio pyramidata* was only recognised in core samples from outside the Red Sea.

Almogi-Labin et al. (1986) studied pteropod shell preservation in a core from the northern Red Sea in relation to stable isotope ratios of carbon and oxygen. They found generally well-preserved shells during glacial stages, and deteriorating preservation during interglacials, with in extreme cases complete dissolution of the aragonite. A last occurrence peak of internal moulds (with or without aragonitic shell) they found at a depth of 0.50 m below sea bottom (lower part of 'Stage 1'). It is supposed that this level was also reached by the boxcores in samples 3 to 6 of the present study. These results led to the application of pteropods as palaeoclimate indicators (Almogi-Labin, 1984; Almogi-Labin et al., 1991, 1998; Hemleben et al., 1996). In a core from the central Red Sea Almogi-Labin et al. (1998, p. 94, fig. 5) found no pteropod moulds and only very few moulds with the original shell preserved. This agrees with the present samples 7–15, in which no internal moulds were observed.

Final note—A further cavoliniid taxon, *Cavolinia gibboides* Rampal, 2002, was recently separated from the well-known species *C. gibbosa* (d'Orbigny, 1836) on the basis of predominantly morphometric characteristics. Its distribution is given as 'en Méditerranée orientale et en Mer Rouge septentrionale (Golfe d'Aqaba)' (Rampal, 2002, p. 221, fig. 4R). In the absence of material for comparison I so far have no well-considered opinion on the validity of the name *C. gibboides*, but there are two reasons making me believe that this species does not occur in the Gulf of Aqaba. First, in the material available for this paper nothing similar to the *C. gibbosa*-group was found to be present, and second, in the specification of material studied by Rampal (pp. 220–221), under the sub-heading 'Golfe d'Aqaba,' only samples from Cyprus are mentioned. This makes me believe that the Gulf of Aqaba occurrence is erroneous.

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Taxonomy of the Family Neilonellidae (Bivalvia, Protobranchia): Miocene and Plio-Pleistocene Species of *Pseudoneilonella* Laghi, 1986 from Italy

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Abstract. *Pseudoneilonella* Laghi, 1986 is considered a valid genus in the family Neilonellidae Schileyko, 1989. It is morphologically similar to *Neilonella* Dall, 1881, but with an external opisthodontic, instead of amphidetic, ligament. In both genera, a small, internal ligament is also present, mainly in the early growth stages. *Austrotindaria* Fleming, 1948 is also considered a valid neilonellid genus. It has an opisthodontic ligament and differs markedly from *Pseudoneilonella* and *Neilonella* by its delicate, poorly sculptured shell. Three bathyal species of *Pseudoneilonella* are known from the Mediterranean Plio-Pleistocene: *Pseudoneilonella pusio* (Philippi, 1844), *P. salicensis* (Seguenza, 1877) and *P. tenella* La Perna, sp. nov. A possible fourth species, *Pseudoneilonella* sp., was present in the Early Pliocene. Another species, *Pseudoneilonella taurinensis* La Perna, sp. nov. is described from the Middle Miocene of the Turin hills. In the European area (paleo-Mediterranean and Paratethys), *Pseudoneilonella* occurs since at least the Middle Miocene. *Pseudoneilonella latior* (Jeffreys, 1876) is a modern representative from the North Atlantic.

INTRODUCTION

The family Neilonellidae Schileyko, 1989 (= Saturniidae Allen & Hannah, 1986, non Boisduval, 1837), of recent institution, includes many species formerly assigned to the Mallettiidae H. & A. Adams, 1858. Some taxonomic studies have been devoted to the Neilonellidae (Maxwell, 1988a; Warén, 1989; Allen & Sanders, 1996; Coan et al., 2000), but this family remains poorly known and without a full agreement about the genera belonging to it (Allen & Hannah, 1986; Maxwell, 1988a; Coan et al., 2000; Allen & Sanders, 1996). Like most protobranchs, neilonellids are mainly distributed in deep waters.

Two neilonellid species were formerly known from the Plio-Pleistocene of Italy, but recent studies shed new light on the composition and stratigraphic distribution of this group. The present paper is a contribution to neilonellid taxonomy, through the study of the fossil species from Italy and focusing on three genera: *Neilonella* Dall, 1881, *Austrotindaria* Fleming, 1948 and *Pseudoneilonella* Laghi, 1986.

MATERIALS AND METHODS

The Plio-Pleistocene bathyal deposits cropping out in Southern Italy (Figure 1) are rich in protobranch bivalves and other typically deep-sea taxa (Di Geronimo & La Perna, 1997; Di Geronimo et al., 1997; La Perna, 2003). The inferred paleodepths range from the slope break to some 1,000 m. The study material is mostly from author's collection, but voucher specimens are deposited in a public institution (MZB). Other

study material is from Middle Pliocene bathyal deposits of Rio Gambellaro, Romagna, Northern Italy (Tabanelli, 1993; Tabanelli & Segurini, 1995), and from the Middle Miocene of the Turin hills (Bellardi & Sacco collection).

The following abbreviations are used: IGNS = Institute of Geological & Nuclear Sciences, National Paleontology collection, Lower Hutt, New Zealand; MCZ = Museum of Comparative Zoology, Harvard University, Cambridge; MRSN = Museo Regionale di Scienze Naturali, Turin; MZB = Laboratorio di Malacologia, Museo di Zoologia dell'Università di Bologna; MZHU = Museum für Naturkunde der Humboldt-Universität, Berlin; coll. = collection; v(s) = loose valve(s); sh(s) = complete shell(s); L = shell length; H = shell height.

SYSTEMATICS

Class Bivalvia Linné, 1758

Subclass Protobranchia Pelseneer, 1889

Order Nuculoida Dall, 1889

Family Neilonellidae Schileyko, 1989

Genus *Pseudoneilonella* Laghi, 1986

Pseudoneilonella was erected by Laghi (1986) as a replacement name for *Saturnia* Seguenza, 1877, non Schrank, 1802, for those species similar to *Neilonella* Dall, 1881 but with an opisthodontic ligament. *Saturnia* and *Pseudoneilonella* are thus objective synonyms with the same type species (ICNZ, art. 67.8), i.e., *Nucula*

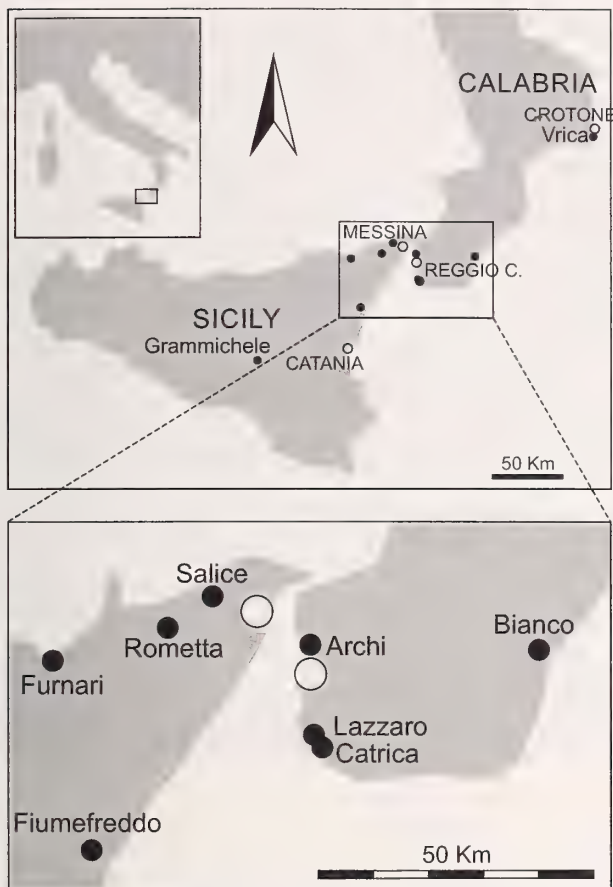


Figure 1. Collecting localities in Southern Italy (solid dots) and references: Vrica, Pliocene/Pleistocene boundary stratotype (Pasini, Colalongo, 1994); Bianco, Early Pleistocene (Di Geronimo, La Perna, 1997); Lazzaro and Catrica, Early-Middle Pleistocene (Di Geronimo, La Perna, 1997); Archi, Early-Middle Pleistocene (Di Geronimo et al., 1997); Salice, Early-Middle Pleistocene (Di Stefano, Lentini, 1995); Rometta, Middle Pliocene (Violanti, 1989); Furnari, Early Pleistocene (Di Geronimo, La Perna, 1997); Fiumefreddo, Early-Middle Pleistocene (Girone et al., 2006); Grammichele (Valle Palione), Early Pleistocene (Girone et al., 2006).

pusio Philippi, 1844 by monotypy (Seguenza, 1877b), in spite of the proposal of *Leda* (*Saturnia*) *pusio* var. *salicensis* Seguenza, 1877 as type species of *Pseudoneilonella* by Laghi (1986). It should be noted that Laghi's opinion of var. *salicensis* Seguenza, 1877 was biased by the misinterpretation of *Nucula pusio* Philippi, 1844 as *Ledella messanensis* (Jeffreys, 1870) (Di Geronimo & La Perna, 1997; La Perna, 2003). In other words, Laghi (1986) did not know the true *Pseudoneilonella salicensis* and applied this name to *Pseudoneilonella pusio*. As summarised by Di Geronimo & La Perna (1997) and La Perna (2003), var. *salicensis* Seguenza is involved in a long history of misidentification (Jeffreys, 1879; Locard, 1889; Laghi, 1986; Warén, 1989; Allen &

Sanders, 1996), which led this name to be applied to a Northeast Atlantic species, *Leda pusio* var. *laticor* Jeffreys, 1876, improperly known as *Neilonella striolata* (Brugnone, 1876) (Warén, 1989; Salas, 1996) or *Neilonella salicensis* (Seguenza, 1877) (Allen & Sanders, 1996).

Dell (1956) and Maxwell (1988a, b) remarked on the differences in the ligament characters of *Neilonella* and *Austrotindaria* Fleming, 1948. *Neilonella corpulenta* (Dall, 1881) (Recent, Caribbean), type species of *Neilonella*, has an external, amphidetic ligament (Figures 2a–e; see also Laghi, 1986: fig. 1c, pl. 9, figs. 1–3; Allen & Sanders, 1996: fig. 11), whereas it is opisthodetic in *Austrotindaria wrighti* Fleming, 1948 (Recent, New South Wales), type species of *Austrotindaria* (Figures 3a–f). Mainly based on this difference, Di Geronimo & La Perna (1997) and La Perna (2003) assigned two species from the Mediterranean Plio-Pleistocene to *Austrotindaria* instead of *Neilonella*, i.e., *Austrotindaria pusio* (Philippi, 1844) and *A. salicensis* (Seguenza, 1877), and considered *Pseudoneilonella* a junior synonym of *Austrotindaria*.

The occurrence in *Austrotindaria* of an edentulous gap in the hinge plate, dividing the tooth series into a posterior and an anterior row, has also been noted in the literature (Fleming, 1948; Dell, 1956; Maxwell, 1988a, b; Beu & Maxwell, 1990). Actually, a short “edentulous gap” occurs in *A. wrighti* (Figures 3c, d), but it consists of a small, elongate ligament pit (not clearly seen from the standard valve orientation), rather than of a smooth portion of hinge plate. This character in no way conflicts with the interpretation of *Austrotindaria* as a neilonellid, since the external ligament of this family develops through an early inner stage (Figures 7b, d, f) and a relict ligament pit can be preserved in the later growth stages, as an internal or external (above hinge) small pit (Figures 2d, e, 7h, i). The development of a short, poorly defined edentulous gap in *Pseudoneilonella* (Figures 7h, k) is probably related to these ontogenetic changes. This character was well described by Verrill & Bush (1898: 877–878) on *Neilonella corpulenta*: “Resilium very minute or nearly abortive, occupying a slight notch in the dorsal margin under the beak, external to the series of teeth, which are interrupted only by a small, thin edentulous space”. It is worth noting that a distinct, apparently functional inner ligament pit is present in the adult stages of small sized species (Figures 6b, g, 8i), suggesting heterochronic relationships between larger and smaller species. The neilonellid inner ligament is thought to be evidence of the affinities between this family and the Malletiidae, which also possess an early inner ligament, migrating outwards with growth (Okelmann & Warén, 1998).

Austrotindaria and *Neilonella* differ from each other profoundly in shell characters and the most obvious

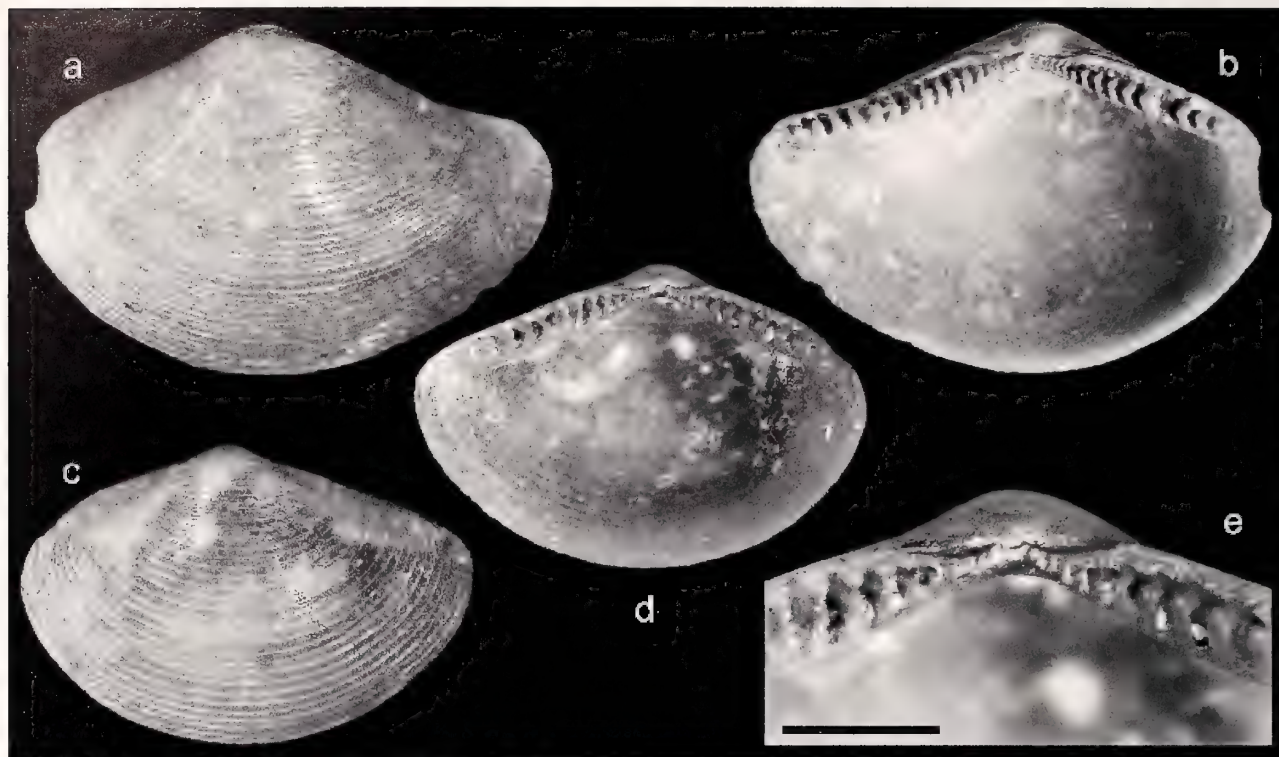


Figure 2. *Neilonella corpulenta* (Dall, 1881), syntypes, Blake Exp., st. 21, Cuba, off Bahia Honda, 525 m, MCZ 007951. a, b. 7.8 mm. c–e. 6.8 mm. Scale bar 1 mm.

difference lies in shell robustness and sculpture strength: the delicate, almost smooth shell of *Austrotindaria* strongly contrasts with the sturdy, sculptured shell of *Neilonella*. No pallial sinus was described for *Austrotindaria*, and examination of the type material failed in detecting a pallial line, sinus and even muscle scars. The species of the family Tindariidae Verrill & Bush, 1897 lack siphons and a pallial sinus (Sanders & Allen, 1977), but their ligament is mainly posterior, widely extending anteriorly and, apparently, with no internal component (Verrill & Bush, 1898; Knudsen, 1970; Sanders & Allen, 1977).

Some Recent and Cenozoic species from New Zealand are assigned to *Austrotindaria*, such as *A. benthicola* Dell, 1956, *A. flemingi* Dell, 1956 (Dell, 1956: pl. 2, figs. 12–15; external views of holotypes are available in the website of the Te Papa Tongarewa Museum, New Zealand) and *A. mawherensis* Maxwell, 1988 (Maxwell, 1988a: pl. 2, figs. 2a, b, d). These species seem to agree with the type species of *Austrotindaria*, except for their weak posterior rostration, which is practically absent in *A. wrighti* ("No indication of rostrum": Fleming, 1948).

Other Cenozoic species from New Zealand are assigned to *Pseudotindaria* Sanders & Allen, 1977 (Maxwell, 1988b, 1992; Beu & Maxwell, 1990). This genus is conchologically similar to *Tindaria* Bellardi,

1875 (family Tindariidae), but differs in possessing siphons (Sanders & Allen, 1977). However, none of the fossil species from New Zealand seems to have the rounded or shortly ovate, poorly inequilateral shell shape of *Pseudotindaria*, as seen in the type species *P. erebus* (Clarke, 1974) (Sanders & Allen, 1977: figs. 29, 31, 39; Warén, 1989: figs. 19a, b). Rather, these species closely match *Pseudoneilonella* in shape, sculpture and ligament characters.

Neilonella and *Austrotindaria* were also applied by Coan et al. (2000) to some protobranchs from Western North America, but the ligament characters were inverted, i.e., opisthodetic in *Neilonella*, amphidetic in *Austrotindaria*. However, none of those species appears to be well allocated in these genera.

Four fossil species from the Mediterranean area, studied in the present work, form a morphologically homogeneous group, markedly similar to *Neilonella* in shell shape and sculpture, but with an opisthodetic ligament. At least two Atlantic living species also belong to this group: *Pseudoneilonella latior* (Jeffreys, 1876) and *P. guineensis* (Thiele, 1931). The shell-ligament system is thought to bear strong characters for limiting related groups within the Protobranchia (e.g., Allen & Hannah, 1986; Warén, 1989; Ockelmann & Warén, 1998) and, as far as is known, there is no gradual transition between the amphidetic condition of

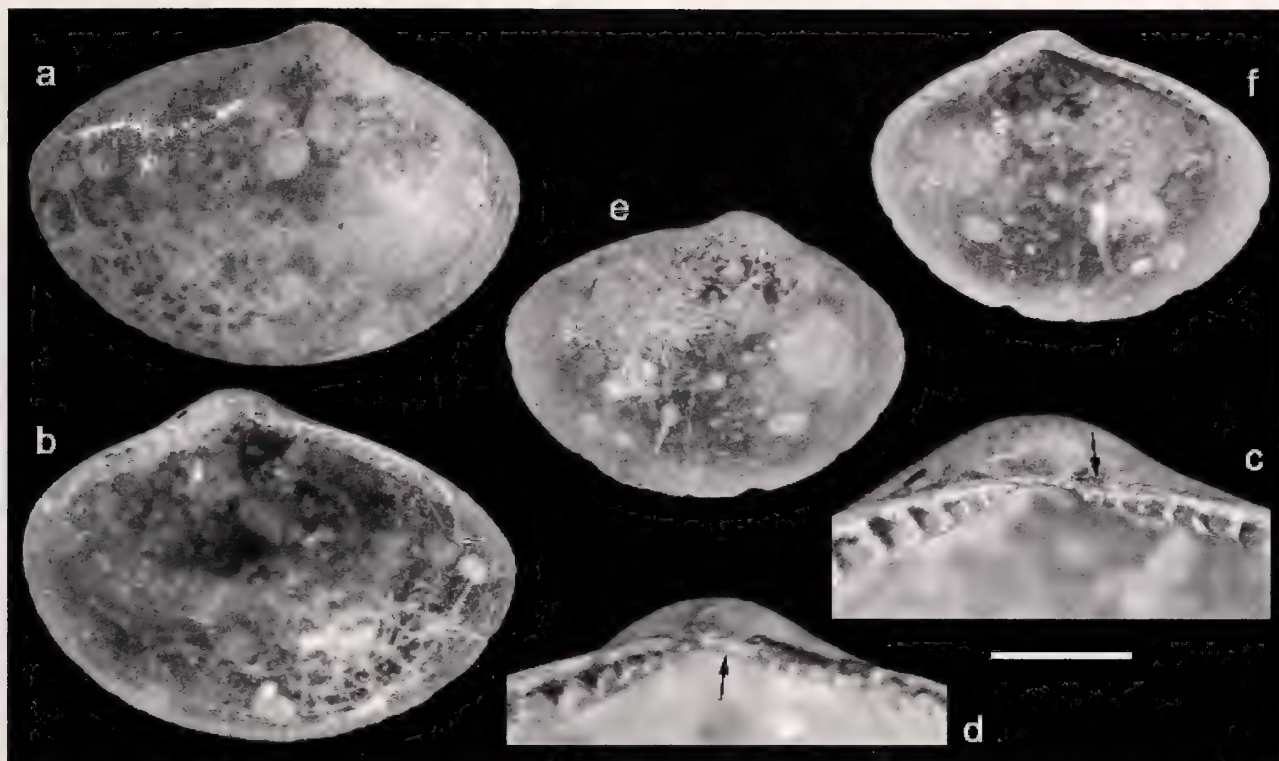


Figure 3. *Austrotindaria wrighti* Fleming, 1948, New Golden Hind Exp., st. 39, Northport, New South Wales, 106 m. a–d. Holotype, 3.6 mm, IGNS, TM109. c,d. standard and oblique views of hinge (note the external posterior ligament in c and the thin, inner ligament pit in d), scale bar 0.5 mm; e, f. Paratype, 2.9 mm, IGNS, TM110. The type material includes a second paratype (left valve) from st. 52, east of Pigeon Island, 40 m (Fleming, 1948: p. 73). It is a different, thin-shelled, subrostrate species with a triangular resiliifer, which can be referred to the genus *Yoldiella* Verrill & Bush, 1897. Apparently, this valve was not used in the description of *A. wrighti*.

Neilonella and the opisthodetic one of *Austrotindaria* and *Pseudoneilonella*. For this group of species, a systematic position in the genus *Pseudoneilonella* is then proposed.

Pseudoneilonella pusio (Philippi, 1844)

(Figures 4a–l, 7a, b, g, h, j–m, o)

Nucula pusio Philippi, 1844: 47, pl. 15, fig. 5.

Pseudoneilonella salicensis Laghi, 1986: 191, pl. 5, figs.

1a, b, 3a, b, 4, 5a, b, 6a, b, 7a–c.

Pseudoneilonella montanaroe Laghi, 1986 (*partim*): 193,

pl. 9, figs. 5a, b, 8a, b (non figs. 4a, b, 6a, b, 7).

Neilonella pusio: Warén, 1989: 252, figs. 16 e, f.

Austrotindaria pusio: Di Geronimo & La Perna, 1997: 414, pl. 9, figs. 1–6, 11.

Types: The type material of *Nucula pusio* (Plio-Pleistocene of Calabria, Southern Italy) is unknown (not present in the Philippi coll. at MZHU: H. Scholz, pers. comm.).

Material examined: Vrica, Pliocene/Pleistocene bound-

ary stratotype, 7 vs. Bianco, Early Pleistocene, 36 vs. Furnari, Early Pleistocene, 74 vs. Fiumefreddo, Early Pleistocene, 132 vs. 3 shs. Archi, Early-Middle Pleistocene, ca 600 vs. 15 shs. Lazzaro, Early-Middle Pleistocene, 126 vs. Catrica, Early-Middle Pleistocene, 69 vs. 2 shs.

Description: Shell small, ovate-trigonal, not very elongate, inequilateral, moderately inflated and sturdy. Umbo small, feebly opisthogyrate, posterior to midline. Postero-dorsal margin long, slightly convex to almost straight; junction with posterior margin subangulate. Antero-dorsal margin short, gently convex, smoothly merging with a well rounded anterior margin. Ventral margin wide, strongly convex. A smooth, obscure keel from umbo to postero-ventral angle, close to dorsal margin. Lunule small, depressed, fairly distinct, escutcheon elongate, poorly defined. Surface with low, fine, closely spaced commarginal ridges, ill defined to lost towards umbo and postero-dorsally. Hinge plate robust, somewhat angled, with chevron-shaped teeth in a single series, sometimes divided into two rows by an ill defined edentulous gap or a small pit. Juveniles with an

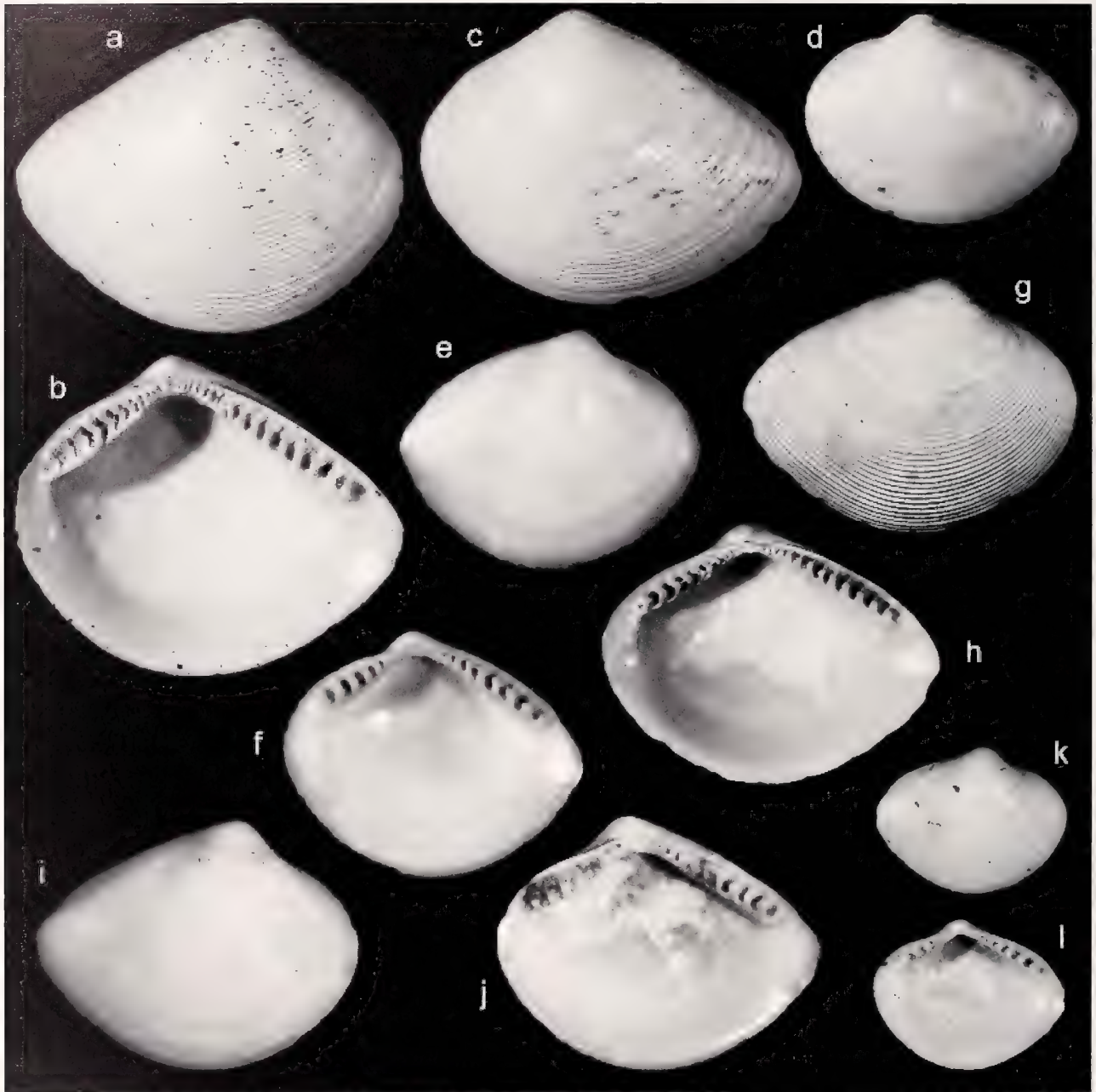


Figure 4. *Pseudoneilonella pusio* (Philippi, 1844). a–f, k, l. Archi, Early-Middle Pleistocene. a, b. 4.5 mm, MZB 29741. c. 4.4 mm, MZB 29741. d. 3.2 mm, MZB 29741. e, f. 3.5 mm, MZB 29741. k, l. 2.3 mm, MZB 29741. g, h. Bianco, Early Pleistocene, 3.9 mm, MZB 29742. i, j. Fiumefreddo, Early Pleistocene, 3.8 mm.

internal, roundish ligament pit beneath beak. Anterior row shorter and stronger than posterior. Externally, a narrow, short ligament furrow, posterior to beak. Adductor muscle scars rounded, generally indistinct. Pallial line forming a wide, not markedly deep posterior sinus. Prodissoconch ovate, about 215 μ m in maximum diameter. Maximum shell size 6.4 mm (L).

Distribution: It is one of the most common proto-branches in the Early to Middle Pleistocene bathyal assemblages (Di Geronimo & La Perna, 1997; Di Geronimo et al., 1998; La Perna, 2003). It was also present, apparently less commonly, in the earliest Pleistocene (Calabrian) and in the latest Pliocene (Gelasian). The occurrence in the older Pliocene needs

confirmation; some Miocene records reported in the past and modern literature are discussed below.

Remarks: *Nucula pusio* was described as a fossil from Bianco (southern Calabria), where Pliocene and Pleistocene clayey deposits with bathyal associations crop out widely (Di Geronimo & La Perna, 1997). The exact location of the original outcrop is unknown and a possible topotype, from Early Pleistocene beds, is here illustrated (Figures 4g, h; see also Di Geronimo & La Perna, 1997: pl. 9, figs. 1, 3, 4, 6, 11). The expression *fovea ligamenti non conspicua* (= ligament pit not visible), in the original description (Philippi, 1844: 47, pl. 15, fig. 5), does not indicate that the species has a “small resilifer” as misinterpreted by Laghi (1986). On the other hand, *Ledella messanensis* (see above) has a distinct ligament pit.

Pseudoneilonella pusio is well characterised by the strongly convex ventral margin and the attenuation of sculpture posteriorly and postero-dorsally.

Pseudoneilonella montanaroe Laghi, 1986 includes *Pseudoneilonella pusio* (from a Pliocene locality in southeastern Sicily) and *P. latior* (NE Atlantic, Jeffreys coll.), both represented by rather juvenile shells (about 3.0 mm in length). Formally, *Pseudoneilonella montanaroe* (emended as *montanaroe*) should be considered a junior synonym of *P. latior*, since the holotype (Laghi, 1986: pl. 9, figs. 6 a, b) is based on this species.

Pseudoneilonella salicensis (Seguenza, 1877)

(Figures 5a–p, 7c–f, n, p)

Leda (Saturnia) pusio var. *salicensis* Seguenza, 1877a: 96.

Leda (Saturnia) pusio var. *salicensis* Seguenza, 1877b: 18, pl. 4, fig. 20.

Austrotindaria salicensis: Di Geronimo & La Perna, 1997: 416, pl. 9, figs. 7–9.

Leda (Saturnia) pusio var. *salicensis*: Bertolaso & Palazzi, 2000: 32, figs. 124, 125 (type).

Types: Museo di Paleontologia dell'Università di Firenze, Seguenza coll., 4 vs (syntypes).

Material examined: Rometta, Middle Pliocene 30 vs, 4 shs. Rio Gambellaro, Middle Pliocene, 50 vs, 9 shs. Vrica, Pliocene/Pleistocene boundary, 67 vs, 24 shs. Salice, Early-Middle Pleistocene, 3 vs.

Description: Shell small, ovate-trigonal, weakly elongate, inequilateral, markedly inflated and sturdy. Umbo large, feebly opisthogyrate, posterior to midline. Postero-dorsal margin long, slightly convex to almost straight; junction with posterior margin subangulate to moderately pointed. Antero-dorsal margin short, gently convex, smoothly merging with a well rounded anterior margin. Ventral margin wide, strongly convex.

A smooth, obscure keel from umbo to postero-ventral angle, close to dorsal margin. Lunule small, depressed, fairly distinct, escutcheon elongate. Surface with low, fine, closely spaced commarginal ridges, becoming weaker to ill defined towards umbo. Hinge plate notably robust, somewhat angled, with chevron-shaped teeth in a single series, sometimes divided into two rows by an ill defined edentulous gap or pit. Juveniles with an internal, roundish ligament pit beneath beak. Anterior row shorter and stronger than posterior. Externally, a narrow, short ligament furrow, posterior to beak. Adductor muscle scars rounded, generally indistinct. Pallial line forming a wide, deep posterior sinus. Prodissoconch ovate, about 215 µm in maximum diameter. Maximum shell size about 5.0 mm (L).

Distribution: The known distribution ranges from Middle Pliocene (Piacenzian) to Early Pleistocene. It is uncommon in the Pleistocene deposits.

Remarks: Di Geronimo & La Perna (1997) proposed an identity for *Leda (Saturnia) pusio* var. *salicensis* on topotypic material from Salice (Messina) and the type material reported by Bertolaso & Palazzi (2000: 32, figs. 124, 125) confirmed this identity.

As originally described, *Pseudoneilonella salicensis* is more inflated and sturdily built than *P. pusio*. The ventral margin is less convex, the hinge angle is slightly wider (125°–129° in *P. salicensis*, 120°–123° in *P. pusio*) and the sculpture is more uniform across the shell surface. Puzzlingly, this species was said by Seguenza (1877b) to be more similar to the Atlantic material sent to him by Jeffreys, than to typical *P. pusio*. The Atlantic species is *Pseudoneilonella latior* (Jeffreys, 1876), which is notably less convex and robust, more ovate and elongate (Warén 1989: figs. 16 a–d; Salas, 1996: figs. 52–54). Probably, Seguenza based his opinion mainly on the shell outline, which is somewhat ovate in *P. salicensis* and *P. latior*, rather than roughly squared as in *P. pusio*.

Pseudoneilonella salicensis is more variable than *P. pusio*, particularly in shell elongation and sharpness of the posterior end. It was not possible to separate some markedly “pointed” shells (Figures 5 l–p) from the others with a blunter posterior end. A similar variability was noted by Verrill & Bush (1898: 879) on *Neilonella subovata* Verrill & Bush, 1897 (= *Pseudoneilonella latior*): “Some [specimens] are decidedly more elongated and tapered posteriorly ... others are somewhat shorter and more regularly ovate with the posterior end blunter or more rounded”.

As discussed above, the present species is neither *Neilonella salicensis* of Laghi (1986) (= *Pseudoneilonella pusio*), nor *Neilonella salicensis* of Allen & Sanders (1996) (= *P. latior*).

Robba (1981: 136, pl. 10 figs. 4–7, pl. 11, fig. 1) reported *Saturnia pusio salicensis* from the Early



Figure 5. *Pseudoneilonella salicensis* (Seguenza, 1877). a-e. Rometta, Middle Pliocene: a, b. 4.4 mm, MZB 29743. c. 3.5 mm, MZB 29743. d, e. 3.1 mm. f-i. Rio Gambellaro, Middle Pliocene. f, g. 4.6 mm. h. 3.7 mm, MZB 29744. i. 2.3 mm. j-p. Vrica, Pliocene/Pleistocene boundary stratotype. j, k. 4.8 mm, MZB 29745. l, m. 3.7 mm. n. 2.3 mm, MZB 29745. o. 2.8 mm. p. 3.1 mm, MZB 29745.

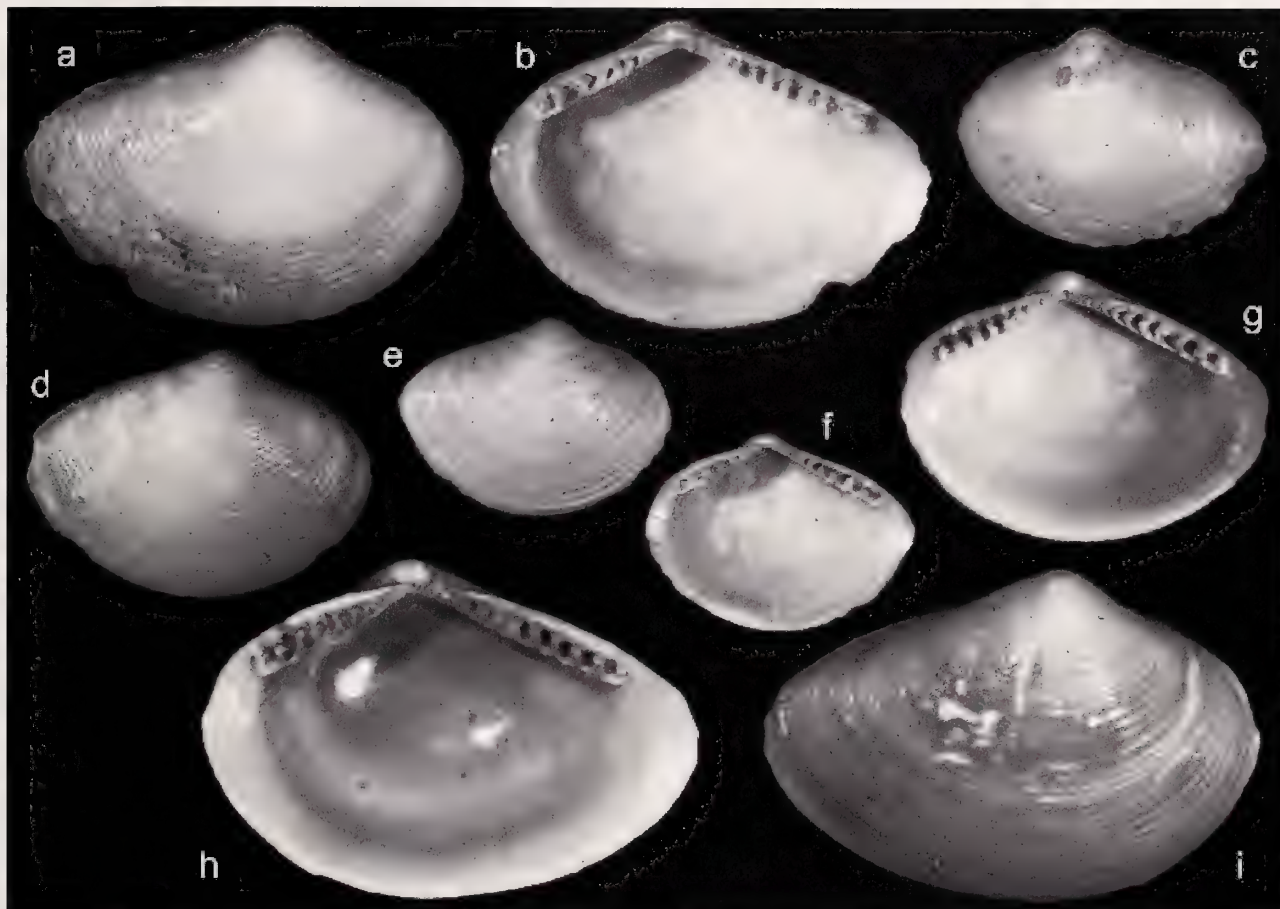


Figure 6. *Pseudoneilonella tenella* La Perna, sp. nov. a–g. Grammichele (Valle Palione), Early Pleistocene: a, b. Holotype, 3.5 mm, MZB 29746. c. Paratype 1, 2.5 mm, MZB 29747. d. Paratype 2, 2.8 mm, MZB 29747. e, f. 2.2 mm. g. 3.0 mm. h, i. Rio Gambellaro, Middle Pliocene, 4.0 mm.

Pliocene of Liguria. Excluding one specimen (pl. 10, figs. 4a, b), which is most probably a species of *Ledella*, the other illustrations actually depict a species of *Pseudoneilonella*, similar in shape to *P. salicensis*, but much smaller (not exceeding 2.5 mm in length) and with a coarser, less dense sculpture. It is probably an undescribed species, here tentatively referred to as *Pseudoneilonella* sp.

Pseudoneilonella tenella La Perna, sp. nov.

(Figures 6a–i, 7i)

Type material: Holotype, MZB 29746 and 2 paratypes, MZB 29747.

Type locality: Grammichele (Valle Palione), southeastern Sicily, Early Pleistocene upper bathyal marls underlying richly fossiliferous coarse sands with *Arctica islandica* (Linné, 1767)

Material examined: Grammichele, Early Pleistocene, 12

vs, 1 sh, including type material. Rio Gambellaro, Middle Pliocene, 2 vs.

Etymology: From the Latin *tenellus* (= diminutive of *tener*, tender, delicate), due to the delicate appearance.

Description: Shell small, ovate, weakly elongate, inequilateral, moderately inflated and thin-walled. Umbo small, leaning out from shell outline, feebly opisthogyrate, posterior to midline. Postero-dorsal margin long, straight to barely convex; junction with posterior margin rounded to obscurely angled. Antero-dorsal margin short, gently convex, smoothly merging with a well rounded anterior margin. Ventral margin wide, convex. Lunule small, depressed, fairly distinct, escutcheon elongate, poorly defined. Surface with low, fine, closely spaced commarginal ridges, slightly coarser anteriorly, poorly defined towards umbo. Hinge plate relatively robust, somewhat angled, with chevron-shaped teeth in a single series, or divided into two rows by a small ligament pit. Anterior row shorter than

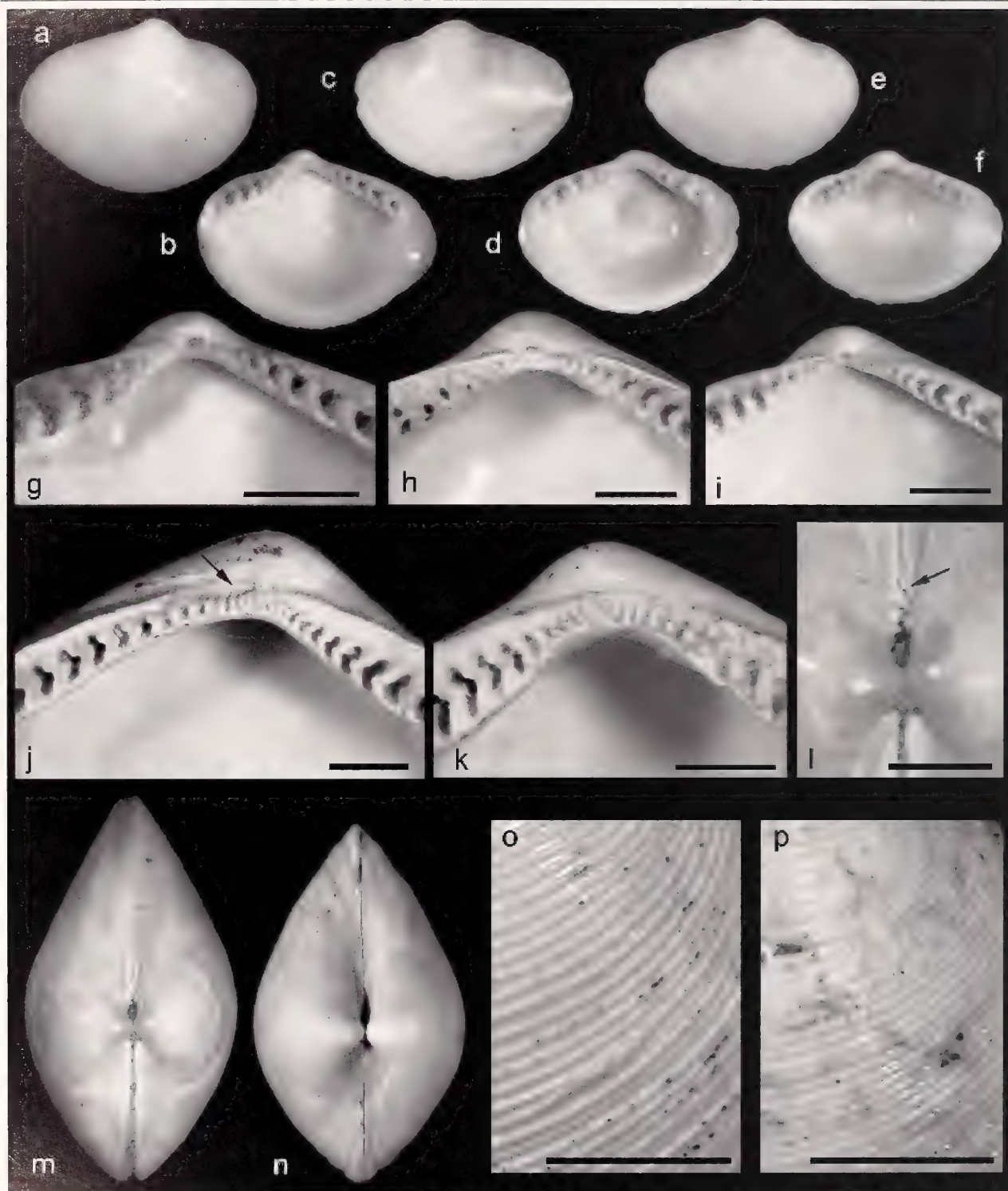


Figure 7. a-f. Juvenile stages. a, b. *Pseudoneilonella pusio*, Archi, 2.3 mm. c-f. *Pseudoneilonella salicensis*. c, d. Rometta, 1.2 mm. e, f. *Vrica*, 1.6 mm. g-l. Details of hinge. g, h. *Pseudoneilonella pusio*. g. Archi, 2.3 mm (same as 7a, b). h. Bianco, 3.9 mm (same as 4g, h). i. *Pseudoneilonella tenella* La Perna, sp. nov., Grammichele (Valle Palione), 3.8 mm (same as 6g). j. *Pseudoneilonella pusio*, Bianco, 4.6 mm (note the well developed external furrow for ligament insertion). k. *Pseudoneilonella pusio*, Archi, 4.5 mm (same as 4a, b). l. *Pseudoneilonella pusio*, Archi, 4.1 mm (note the external posterior ligament furrow through which dentition is seen). m. *Pseudoneilonella pusio*, Archi, 4.1 mm. n. *Pseudoneilonella salicensis*, *Vrica*, 3.9 mm. o, p. Sculpture details, anterior side. o. *Pseudoneilonella pusio*, Archi. p. *Pseudoneilonella salicensis*, *Vrica*. Scale bars 0.5 mm.

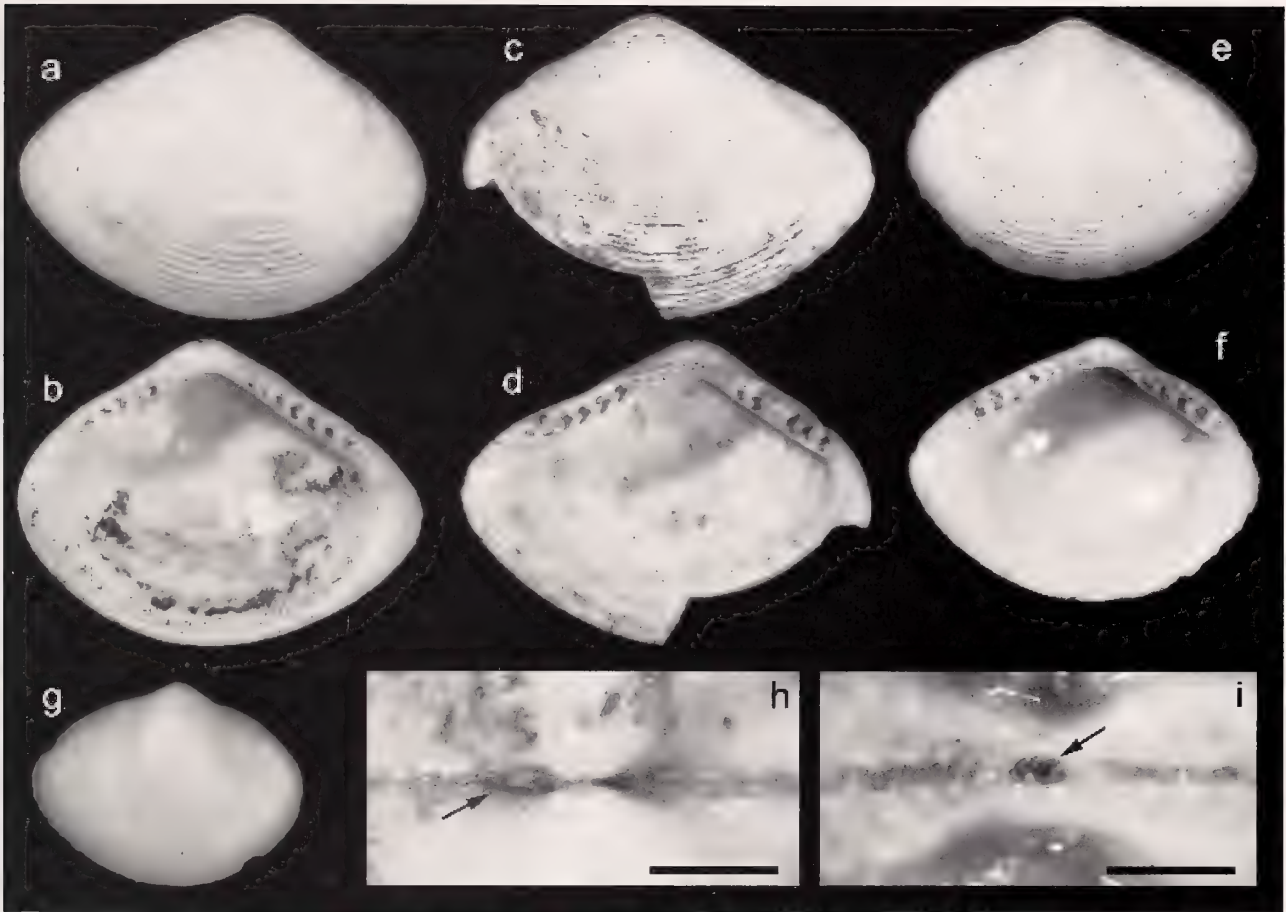


Figure 8. *Pseudoneilonella taurinensis* La Perna, sp. nov. a–i. Monte dei Cappuccini, Turin hills, Langhian, MRSN, Bellardi & Sacco coll., BS 123.04.09/03. a, b. Holotype, 2.7 mm. c, d. Paratype 1, 2.7 mm. e, f. Paratype 2, 2.3 mm. g. Paratype 3, 1.8 mm. h, i. Umbonal fragment of a closed shell, external and internal view (note the external ligament furrow and the internal ligament pit). Scale bars 0.5 mm.

posterior. Externally, a narrow, short ligament furrow, posterior to beak. Adductor muscle scars rounded, generally indistinct. Pallial line forming a wide, not particularly deep posterior sinus. Prodissoconch ovate, about 200 μ m in maximum diameter. Measurements: holotype 3.5 mm (L), 2.4 mm (H); paratype 1, 2.5 mm (L), 1.8 mm (H); paratype 2, 2.8 mm (L), 2.0 mm (H).

Distribution: Middle Pliocene to Early Pleistocene, but the Pliocene record needs confirmation.

Remarks: *Pseudoneilonella tenella* La Perna, sp. nov., formerly tentatively treated as a shallower ecotype of *Pseudoneilonella pusio* (La Perna, 2003), differs from *P. pusio* and *P. salicensis* by being more delicate, less convex and smaller. The umbo is clearly distinctly above the shell outline. It is somewhat similar to *Pseudoneilonella latior*, from which it differs mainly by being much smaller, less elongate and with a more prominent umbo.

The scarce material from the Middle Pliocene of Romagna differs subtly from the Pleistocene material, by being slightly larger and more inflated, with a better defined posterior rostration and a less dense sculpture. This material is tentatively referred to as *Pseudoneilonella tenella* La Perna, sp. nov. but more material is needed for better understanding its taxonomic status.

Pseudoneilonella taurinensis La Perna, sp. nov.

(Figures 8a–i)

Type material: Holotype and 5 paratypes, MRSN, Bellardi & Sacco coll. (ex Forma coll.), BS 123.04.009/03.

Type locality: Monte Cappuccini, Turin hills, Langhian.

Material examined: The types and 21 vs, 8 shs from the type locality. Sciolze and Pian dei Boschi, Turin hills,

generic Early-Middle Miocene, MRSN, Bellardi & Sacco coll. (ex Rovasenda coll.), BS 123.04.009/02, 7 shs.

Distribution: Middle Miocene (Langhian), Turin hills.

Etymology: After *taurinensis* (= from Turin), Latin.

Description: Shell minute, ovate-trigonal, weakly elongate, inequilateral, moderately inflated and robust. Umbo small, feebly opisthogyrate, posterior to midline. Postero-dorsal margin long, slightly concave to almost straight; junction with posterior margin subangulate. Antero-dorsal margin short, gently convex, smoothly merging with a well rounded anterior margin. Ventral margin wide, strongly convex. Lunule small, depressed, fairly distinct, escutcheon elongate, poorly defined. Surface with low, fine, closely spaced commarginal ridges, evenly distributed from umbo to ventral margin. Hinge plate relatively robust, somewhat angled, with chevron-shaped teeth in two series, separated by a small, slightly elongate ligament pit. Anterior row slightly shorter than posterior. Externally, a narrow, notably short ligament furrow, posterior to beak. Adductor muscle scars rounded, generally indistinct. Pallial line forming a rather wide sinus. Prodissoconch ovate, about 170 μm in maximum diameter. Measurements: holotype 2.7 mm (L), 2.0 mm (H); paratype 1, 2.7 mm (L), 2.0 mm (H); paratype 2, 2.3 mm (L), 1.8 mm (H); paratype 3, 1.8 mm (L), 1.3 mm (H). Maximum shell size about 3.0 mm (L).

Remarks: The finding of neilonellid material in the Bellardi & Sacco coll. was totally unexpected. The record of *Neilonella pusio* by Sacco (1898) from the Late Miocene of Northern Italy is based on a manuscript record by Doderlein of a distinct species belonging to the genus *Ledella* Verrill & Bush, 1897 (Laghi, 1986). The present material was labelled as *Jupiteria broccii* (Bellardi, 1875), a much larger species, of which this material was believed to be a juvenile stage.

Pseudoneilonella taurinensis La Perna, sp. nov. looks almost like a miniature of *P. pusio* in shell shape, inflation and robustness. However, the juvenile stages of the latter (Figures 4k, l) are much smoother, ovate and thin shelled.

The type material is from Langhian deposits (Ferrero Mortara et al., 1982; Pavia, 2000, 2003), whereas the other material is from two localities of generic Early-Middle Miocene age (Ferrero Mortara et al., 1982). The hills rising southwest of Turin consists of a thick succession, Oligo-Miocene in age (Clari et al., 1994). The Early-Middle Miocene succession is characterised by coarse grained beds, due to gravity flows, containing a shallow water fauna and intercalated in marly and silty bathyal deposits (Pavia, 2000, 2003). Most molluscs in the Bellardi & Sacco coll. are from the

allochthonous assemblages, as indicated by the sandy sediment filling the shells. Also the material of *Pseudoneilonella taurinensis* La Perna, sp. nov. is filled with a quartzose-micaceous sand, suggesting an allochthonous origin, i.e., from shallow waters. This contrasts with the Plio-Pleistocene and modern deep water distribution of *Pseudoneilonella*, but other data from the Middle Miocene of Paratethys (see below) suggest a change in the bathymetric distribution of this genus.

Hörnes (1865: 304, pl. 38, figs. 6a–e) reported *Leda pusio* (Philippi) from the Badenian (Middle Miocene) of the Czech Republic (Paratethys). This material was recently illustrated by Schultz (2001: 16, pl. 1, figs. 10, 11) and examined on photographs kindly supplied by O. Schultz. It seems to consist of two species, most probably undescribed and belonging to *Pseudoneilonella*. “*Saturnia pusio*” has also been reported from the Badenian of Austria by Studenka et al. (1998) and Zuschin et al. (2004), from shallow water deposits. The record by Zuschin et al. (2004) was proved to be based on a distinct species, *Leda reussi* Hörnes, 1865 on photographs kindly supplied by M. Zuschin.

CONCLUDING REMARKS

Three, or possibly four bathyal species of *Pseudoneilonella* were present through the Plio-Pleistocene in the Mediterranean area (Figure 9). The increased diversity of neilonellids since the Middle Pliocene seems in agreement with the hypothesis of enhanced psychrospheric conditions and increased diversity of the deep-sea fauna since the Piacenzian, as proposed by La Perna (2003, 2004) but, admittedly, the knowledge of the Early Pliocene bathyal fauna is still rather poor, compared with that of the younger fauna.

In the North Atlantic, *Pseudoneilonella* is represented by *P. latior* (Jeffreys, 1876) ranging from North America, southeastern Greenland and south Iceland to the Ibero-Moroccan Gulf (Warén, 1989; Allen & Sanders, 1996; Salas, 1996). It was also present in the Mediterranean during the Late Glacial, as indicated by old valves in the Tyrrhenian Sea (Di Geronimo & La Perna, 1997: pl. 9, fig. 10). *Pseudoneilonella guineensis* (Thiele, 1931) from West Africa, is similar to *P. pusio*, but notably larger (up to 10 mm in length), more elongate and posteriorly sharper (Knudsen, 1970: fig. 39; pl. 6, figs. 8–10). Two other possible species of *Pseudoneilonella* were described by Allen & Sanders (1996): *Neilonella hampsoni* from the Sierra Leone Basin, and *N. whoii* from the North America Basin.

The origin of the Mediterranean and North Atlantic species of *Pseudoneilonella* is not clear. The occurrence of this genus in Europe (paleo-Mediterranean and Paratethys) ranges back to the Middle Miocene at least. A revision of the Middle Eocene-Pliocene species from New Zealand assigned to *Pseudotindaria* (Maxwell,

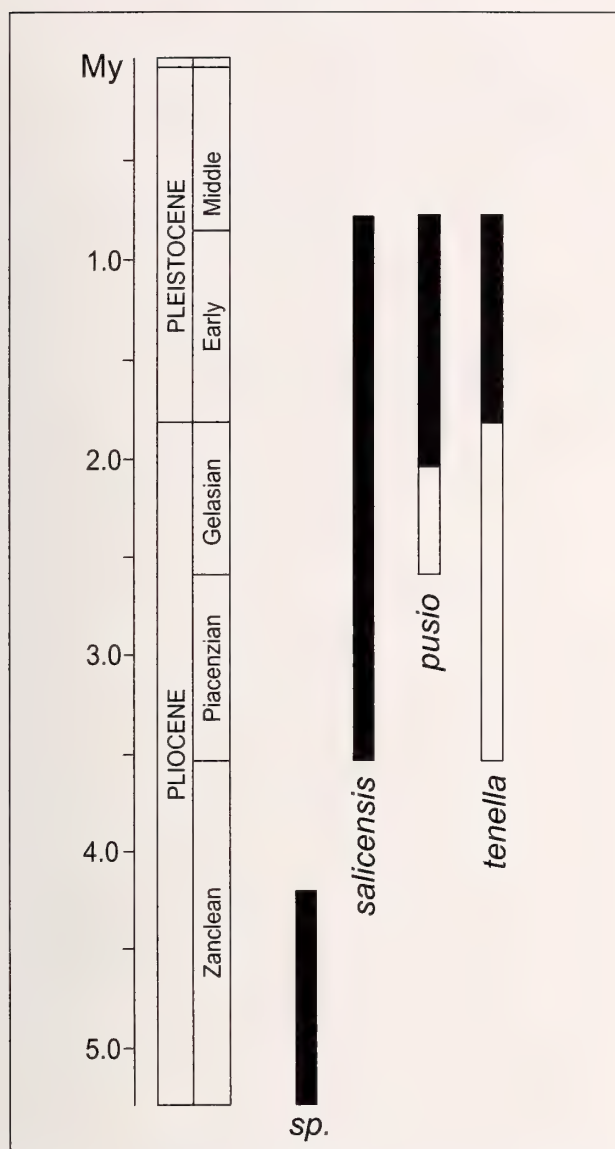


Figure 9. Stratigraphic distribution of the Mediterranean Plio-Pleistocene species of *Pseudoneilonella*. Blank bars indicate dubious data of distribution. Extinctions are arbitrarily positioned at the Early/Middle Pleistocene boundary.

1988b, 1992; Beu & Maxwell, 1990) would be useful to ascertain if they really belong to *Pseudoneilonella*, as suggested in the present work. This may support the hypothesis of a westward diffusion of *Pseudoneilonella*, from the Western Tethys sectors, as proposed for other deep sea European protobranchs (La Perna et al., 2004; La Perna, 2007). Also the study of the Paratethys material could bring useful data to reconstruct the paleogeographic and evolutionary history of *Pseudoneilonella*.

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SHORT NOTE

Sexual Dimorphism in Soft Body Weight in Adult *Monetaria annulus* (Family Cypraeidae)

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Abstract. Sexual size dimorphism in the family Cypraeidae has been questioned due to the use of inappropriate morphometric and statistical methodologies but is demonstrated here for the first time by analysis of the soft body weight of *Monetaria annulus* (Linné, 1758) specimens collected from two distinct populations.

Cowries (Family Cypraeidae) are particularly suitable for investigating molluscan body size variation because of their stepwise shell growth. The soft body enlarges only during the juvenile stage when the shell is fragile and has a coiled structure. This is followed by the deposition of calcareous material on the surface of the juvenile shell to construct a callus. As with some other gastropods (Vermeij and Signor, 1992), cowries are determinate growers in the sense that neither soft body nor callus thickness exhibits any further increase after the callus-building stage.

A number of authors have examined whether sexual size dimorphism (SSD) exists in cowries by measuring shell length, defined as the maximum distance between the anterior and posterior shell tips of adult individuals. Statistically significant differences have been detected between the sexes in *Umbilia hesitata* (Iredale, 1916) (see Griffiths, 1961a), *Erronea erronea* (see Griffiths, 1961b), and *Monetaria caputserpentis* (Linné, 1758) (see Omi and Kuramochi, 2002), but not in *Purpuradusta fimbriata* (Gmelin, 1791) (see Dayle, 1990), *Purpuradusta gracilis* (Gaskoin, 1849) (see Griffiths, 1961a), *Monetaria moneta* (Linné, 1758), *Erosaria helvola* (Linné, 1758) (see Schilder and Schilder, 1961), *Notocypraea angustata* (Gmelin, 1791) (see Griffiths, 1961b), or *Monetaria caputdraconis* (Melvill, 1888) (see Osorio et al., 1999). With regard to *M. annulus*, statistically significant SSD has been detected in one study (Katoh, 1989) but not in two others (Schilder and Schilder, 1961; Lorenz, 2000). One possible reason for such inconsistency is the pooling of specimens from a large area because, regardless of their sex, *M. annulus* can exhibit significant size differences between patches only a few dozen meters apart as the result of

environmentally heterogeneous microhabitats (Irie, 2006). This is a statistical power issue, particularly when sample sizes are small. Another concern is the use of shell length as a proxy for soft body size because shell length continues to increase with the posterior callus development throughout the callus-building stage. Thus, even if shell length is statistically different between sexes, one cannot rule out the possibility that callus thickness, rather than soft body size, exhibits a sexual difference. Conversely a SSD of, for example, a larger soft body in females could be masked by a larger callus thickness in males resulting in no significant sexual difference in shell length. In order to overcome these methodological problems, the SSD in *M. annulus* was examined from two populations from Okinawa, Ryukyu-shoto, Japan.

One hundred adult *Monetaria annulus* were randomly collected from each of two 10 × 10 m² quadrats, one placed at Sesoko (N26°38'20.4", E127°52'07.3") on November 21, the other at Yamada (N26°26'06.0", E127°47'09.7") on November 23, 2006. The shell length, width, and height of each specimen were measured with calipers (Figure 1) and then the shell was broken and removed from the soft body with tweezers, including all fragments. After determining the sex, the soft body was dried by heating for 2 hr at 100°C in a dehydrator and then weighed. The sex ratio did not significantly differ from 1:1 in either Yamada (45 females, 55 males; binomial test, $P = 0.315$) or Sesoko (48 females, 52 males; $P = 0.764$). Mean dry weights (\pm population standard deviation) were 0.598 g (± 0.082) for females and 0.535 (± 0.081) for males in Yamada and 0.678 (± 0.103) for females and 0.646 (± 0.090) for males in Sesoko (Figure 2A).

For each location, data for male and female dry weight were standardized according to their respective z-scores and then pooled. The dry weight was not

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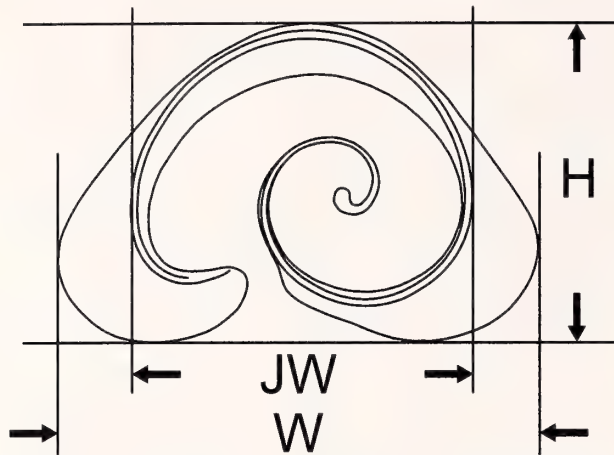


Figure 1. Cross-section of the shell of adult *Monetaria annulus*. Abbreviations: W, adult shell width; H, adult shell height; JW, juvenile shell width.

found to be normally distributed in either Yamada (Shapiro-Wilk test, $W = 0.933$, $P < 10^{-4}$) or Sesoko ($W = 0.943$, $P < 0.001$). However, weight is expected to scale with volume and the cube root of dry weight was found to be normally distributed in both Yamada ($W = 0.983$, $P > 0.05$) and Sesoko ($W = 0.975$, $P > 0.05$). Subsequent parametric tests were conducted on the cube root of dry weight, simply referred to as “dry weight” in the following analysis. The data were divided into four groups according to sex and location. In order to assess the homogeneity of variance, the absolute deviation from the group mean was calculated for each datum. Two-factor crossed ANOVA on the absolute deviation with sex and locality as fixed effects indicated that the variance was positively correlated to the mean between localities ($P = 0.012$). After applying a logarithmic transform to ensure homogeneity of variance (Sokal and Rohlf, 1995), two-factor crossed ANOVA on the dry weight showed that both locality and sex had significant effects (locality, $P < 10^{-11}$; sex, $P < 0.001$) but the locality \times sex interaction did not ($P > 0.05$). Although dry body weight is the most reliable indicator of sexual size dimorphism, for comparison adult shell length was also analyzed. Two-factor crossed ANOVA indicated that females have significantly larger shells. Locality and sex both had significant effects (locality, $P < 10^{-17}$; sex, $P < 0.01$) but the locality \times sex interaction did not ($P > 0.05$). In order to examine the relationship between soft body weight and juvenile shell size, the juvenile shell width (JW; Figure 1) was estimated from the adult shell width (W) and height (H) using an allometric equation proposed by Irie (2006). The correlation (r) between dry weight and estimated JW was 0.891, significantly different from zero ($P < 10^{-15}$). The relative callus

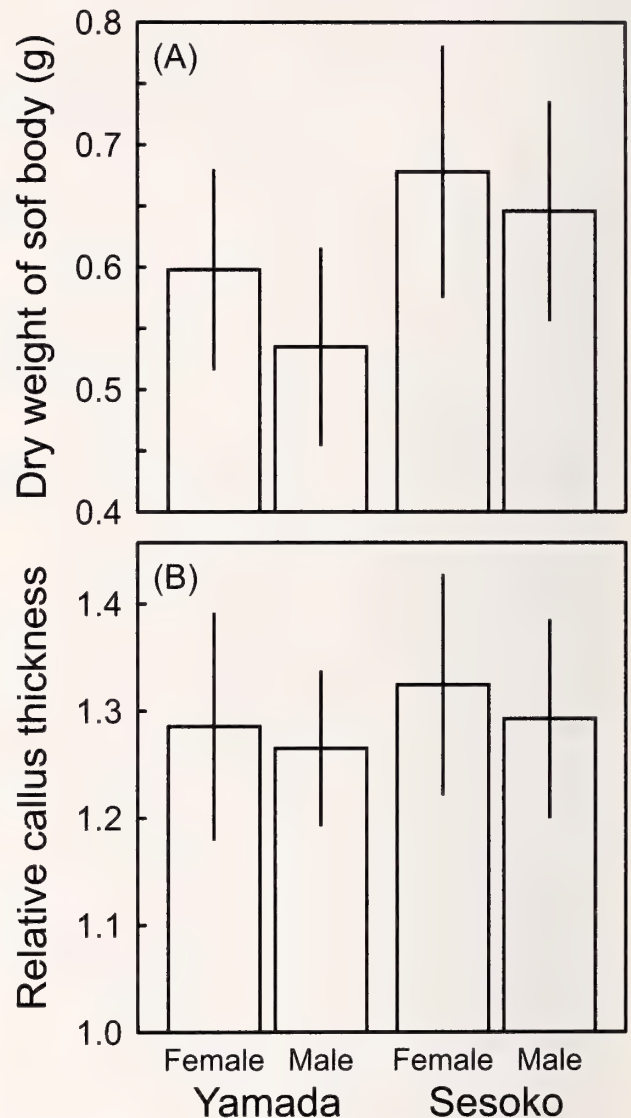


Figure 2. (A) Dry weight of soft body and (B) relative callus thickness (RCT), calculated as shell width/estimated juvenile shell width (W/JW), of the female and male *Monetaria annulus* collected from Yamada and Sesoko coasts of Okinawa, Ryukyu-Soto, Japan. Error bars indicate standard deviations.

thickness (RCT) of each individual, W/JW , was also calculated. This was preferred to the absolute callus thickness, $W - JW$, because it cancels the effect of overall size differences among individuals. Mean RCT was larger in females than males in both localities (Figure 2B). Two-factor crossed ANOVA on RCT indicated that the effect of locality was significant ($P = 0.014$), the effect of sex was marginally non-significant ($P = 0.051$) and the effect of the locality \times sex interaction was not significant ($P > 0.05$).

In conclusion, *Monetaria annulus* exhibits sexual size dimorphism such that females have a larger soft body

than males. The difference in relative callus thickness between males and females was not found to be significant, though only marginally, and this SSD could also be detected from adult shell length. Thus SSD in *Monetaria annulus* is probably not masked by callus size but can easily be masked by environmentally determined size variation when specimens from several distinct areas are pooled.

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Book Review

Marine and Brackish Water Gastropoda of Russia and Adjacent Countries: an Illustrated Catalogue

by YU. I. KANTOR & A. V. SYSOEV. 2006. KMK Scientific Press Ltd. Moscow. 2006. 371 pp., 140 col. pls. In Russian and English. Price: 85€ (available: www.backhuys.com). Moscow

Knowledge of the molluscan fauna of Russia has recently grown by leaps and bounds, starting with the publication in English of a checklist of the shell-bearing gastropods of the northwestern Pacific by Golikov et al. (2001). This was followed by a complete (Russian only) checklist of all mollusks of Russia by Yuri Kantor & Alexander Sysoev (2005), with the assistance of a number of specialists. Only one year later, the same two authors (with authorship for opisthobranchs by E. M. Chaban and A. V. Martinov) have published the *Illustrated Catalog* for the Gastropoda, the first of several intended illustrated catalogs for the Russian species. This new work is large format (A4), sturdily bound, fully bilingual, with columns of Russian and English on the same page, treating all of the marine and brackish water species occurring in the Russian Federation.

Russia covers more than half the entire coastline of the Arctic Ocean, extending from the Barents Sea north of Europe and across Siberia to the Chukchi Sea. South of the Bering Strait it extends to the borders with Japan and North Korea, a region collectively known as the Russian Far East. Also treated within the same systematic framework are the species of a more isolated area, the Black Sea and the landlocked Caspian Sea, having faunal affinities to that of the Mediterranean Sea, but sharing no species with the Barents Sea. That fauna is particularly rich in species of hydrobiids.

The inclusion of the fauna of the Barents Sea and other Arctic seas of Russia improves upon the illustrations in a review (in English) of Arctic gastropods by Golikov (1995) and a checklist (in English) of all invertebrates (Sirenko ed., 2001). The Atlantic Arctic and the north Pacific Arctic have differing species, although there are some widely distributed, circumpolar Arctic species. All are included; thus, this book also serves to provide an updated illustrated catalog of most of the Arctic gastropod species, making it possible to understand the distinctions between the north Atlantic and the north Pacific components.

Until now, illustrations for many Russian species have been of varying quality and detail, but here, for

the first time are color illustrations for the entire marine gastropod fauna of Russia. Among many others Russian authors, I was especially pleased to see excellent illustrations of all species described by Middendorff from 1848–51 and of the species of Golikov and his collaborators from 1962–2004. The figures are of high resolution, large-sized, on a white background, produced from digital images, chiefly of type specimens, with one or sometimes two specimens illustrated for each species. The standard format includes mention of synonyms, original citation with pagination and figures, type locality and original depth, museum catalog number for the primary types, and distribution and depths within Russian territory, and in some cases, remarks that point out errors of misidentification of earlier Russian authors. The plates fill the page, with captions below; the captions give the localities only in English, including the initials of the individual responsible for the identification, usually the authors of earlier revisions. Literature is complete for all authors of treated species, but not for authors of genera or species considered as synonyms. For the Russian literature, users will appreciate that all citations are first given with the English translation of the reference, followed by the Russian citation.

The title of the book makes it clear that this is an illustrated catalog of Russian species. It is not a taxonomic revision, nor is it a general guide to the fauna, because it provides no diagnoses, nor comparisons at any taxonomic level. No taxonomic innovations or new taxa are introduced in this book. However, for its importance to taxonomic and faunistic research, it provides exactly what is needed.

Users of this book should keep in mind a number of limitations of the format, which lacks certain details that might be expected in a revision: Illustrations are not cross-referenced to the text. Captions for type specimens do not repeat the localities provided in the text. Type localities and type material for synonyms are not provided. Citations and references to current revisions are not included. Provenance of type species is not mentioned; pagination and references for genera are not provided. Some frequently used subgenera are not used. The table of contents includes the separate authorship for taxonomic groups; a full systematic arrangement of families is given on page 13, but the reader will have to install the pagination by hand.

Distributions are limited to geographic regions

within Russian territories; however, many of the species have type localities from other regions. A number of included species extend east into Alaskan waters, and even more extend south into Japanese waters. No mention is made of occurrence of the species in Hokkaido or northern Honshu, which are latitudinal equivalents to the southernmost Russian mainland along the northern Sea of Japan. Fortunately, the Japanese molluscan fauna is now reasonably well known as a result of the checklist of Higo et al. (1999), the Japanese types photographed by Callomon (Higo et al., 2001), and the faunal guide of Okutani and his separate contributors (Okutani et al., 2000).

In a separate publication, Kantor & Sysoev (2005) have provided an analysis of biodiversity in which they compared the species diversity of the Russian parts of the Japan Sea, the South, Middle and North Kurile Islands, the Okhotsk Sea, the Bering Sea, and the Chukchi Seas. The counts for these seas overlap. The total count of shelled gastropod species for the Russian Far East is around 700 species (Kantor, pers. comm.) The most speciose group is the family Buccinidae, with over 200 species, with turritiform conids and muricids in second and third places.

The arrangement of families follows that adopted in the "Working Classification" of Gastropoda, introduced by collaborations of Bouchet with Warén ("archaeogastropods"), Ponder (caenogastropods), and Valdés (opisthobranchs), in Part 2 of Bouchet & Rocroi (2005). In that work, higher classification was replaced with unranked clades, within which superfamilies were arranged alphabetically, under which families were also arranged alphabetically, except for the first position of the nominate family. Adherence to the alphabetic arrangement resulted in the positioning of the calyptraeids ahead of the littorinids, which I found disconcerting. Within the major clades I think that an arrangement based on first appearance in the fossil record, or on increasingly derived states would be more informative than one based on alphabetic happenstance.

As the authors note in the introduction, the assessment of global biodiversity is a task of high priority for systematists worldwide. Kantor and Sysoev are in the process of bringing the fauna of Russia to a state of understanding that places it in a comparable position to the fauna of Japan and Europe. Systematists in many of the best known areas of the world, including the Western Atlantic, the European, and the tropical Indo-Pacific are now in the process of data-basing their molluscan faunas for online access.

Here I note that except for the bivalves reviewed by Coan, Scott, & Bernard (2000), an understanding of the mollusks of the northeastern Pacific, which was once considered a well-known fauna, now lags far behind

that of the above mentioned areas. I have long been working on a revision/review of the northeastern Pacific gastropods, including the descriptions of new species, to be published in two books, the first treating the species of British Columbia south to central Baja California, and the second treating those of Alaska, as well the species of north Pacific from the Russian Far East, and also including those British Columbia. For the northern species, it has always been apparent that a limit to the eastern Pacific as marked by the Bering Strait is artificial, because the Alaskan fauna extends west along the northern reaches of the Bering Sea (in Russian territory) and also extends west through the Aleutian Islands (in U.S. territory). The species of the Russian Far East are in many cases the same, or are mostly comparable at the generic level. Now, thanks to the *Illustrated Catalogue* of Kantor & Sysoev, it possible for me to treat the entire shelled gastropod fauna of the northern Pacific.

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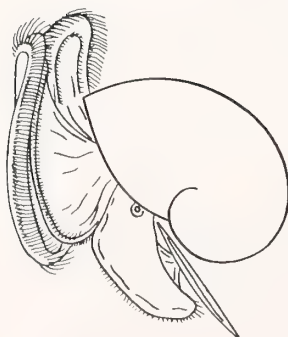
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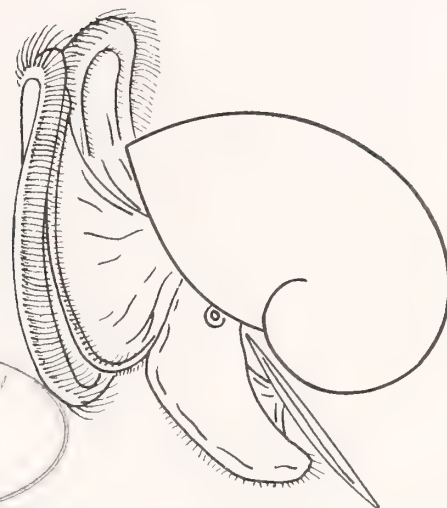


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THE VELIGER

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The Veliger is an international, peer-reviewed scientific quarterly published by the California Malacozoological Society, a non-profit educational organization. *The Veliger* is open to original papers pertaining to any problem connected with mollusks. Manuscripts are considered on the understanding that their contents have not appeared, or will not appear, elsewhere in substantially the same or abbreviated form. Holotypes of new species must be deposited in a recognized public museum, with catalogue numbers provided. Even for non-taxonomic papers, placement of voucher specimens in a museum is strongly encouraged and may be required.

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Nipponolimopsis littoralis, a New Species from Intertidal Boulder Shores in Japan, with a Systematic Review of the Genus (Bivalvia: Limopsoidea)

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Abstract. *Nipponolimopsis littoralis* n. sp. is described from the Pacific coast of central Japan and compared with other Recent and fossil species of the genus. The new species is distinguished from other members of the genus mainly in having (1) the periostracum composed of thick radially arranged bristles and thin commarginally lamellate membranes, (2) an obliquely oval outline without prominent posteroventral extension, (3) the hinge with three anterior and four posterior teeth, and (4) a finely pitted prodissococonch with a central depression and a marginal thickening. In addition, the habitat of the new species in the intertidal bolder shores is strikingly different from that of other lower subtidal species. This is the only species of *Nipponolimopsis* recorded from the intertidal zone.

INTRODUCTION

The superfamily Limopsoidea comprises two families, Limopsidae and Philobryidae. The former is most successfully adapted to the subtidal to bathyal zone and also extends into abyssal depths (5,000 m and deeper) (e.g., Kundsén, 1970; Oliver & Allen, 1980; Oliver, 1981; Coan et al., 2000; Matsukuma, 2000; Amano & Lutaenko, 2004), while the latter is generally confined to the intertidal to shallow subtidal zones (Tevés, 1977; Powell, 1979; Hayami & Kase, 1993; Lamprell & Healy, 1998; Coan et al., 2000; Malchus, 2006). Most limopsids prefer soft sediments, either being attached to coarse grains with a byssus or freely buried in sands or mud (e.g., Kondo, 1989); some species are epibyssately attached to hard substrates (Oliver, 1981: fig. 3), but such a mode of life is uncommon. The habitats of Philobryidae are less well examined, and philobryids have been recorded mainly from shallow-water rocky bottoms, including submarine caves.

The genus *Nipponolimopsis* has been treated as a member of the Limopsidae by most authors based on overall shell morphology (see below for details). The previously known species of the genus have been all collected from the lower subtidal zone, which seems consistent with the distinction between shallow-water philobryids and deeper-water limopsids. However, in

field sampling on the main island of Japan, we have collected an unidentified limopsid-like species from the undersides of boulders in the intertidal zone. Morphological observations revealed that it belongs to the genus *Nipponolimopsis* which has never been known from the intertidal zone. We describe this new species, review the records of previously known species of the genus, and discuss their taxonomic characters and implications for limopsid systematics.

MATERIAL AND METHODS

The samples of a new species were collected from the undersides of boulders in the intertidal zone in Cape Manazuru, Kanagawa Prefecture (type locality: Figures 1, 2) and other localities (Figure 2). The shells with or without an intact periostracum were photographed with a binocular microscope and a scanning electron microscope (SEM: Hitachi S-2250N). The muscle scars inside of the shell are unclear in fresh specimens, but they were easily visible after the shell is soaked in 10% formalin for one day. Gross anatomy was investigated based on 22 samples: Two samples were collected from Oizura, Kitaibaraki City, Ibaraki Prefecture, five from Isozaki, Hitachinaka City, Ibaraki Prefecture and the other 15 from Tsumeki-zaki, Shimoda City, Shizuoka Prefecture. Live animals were relaxed in 7.5% MgCl₂

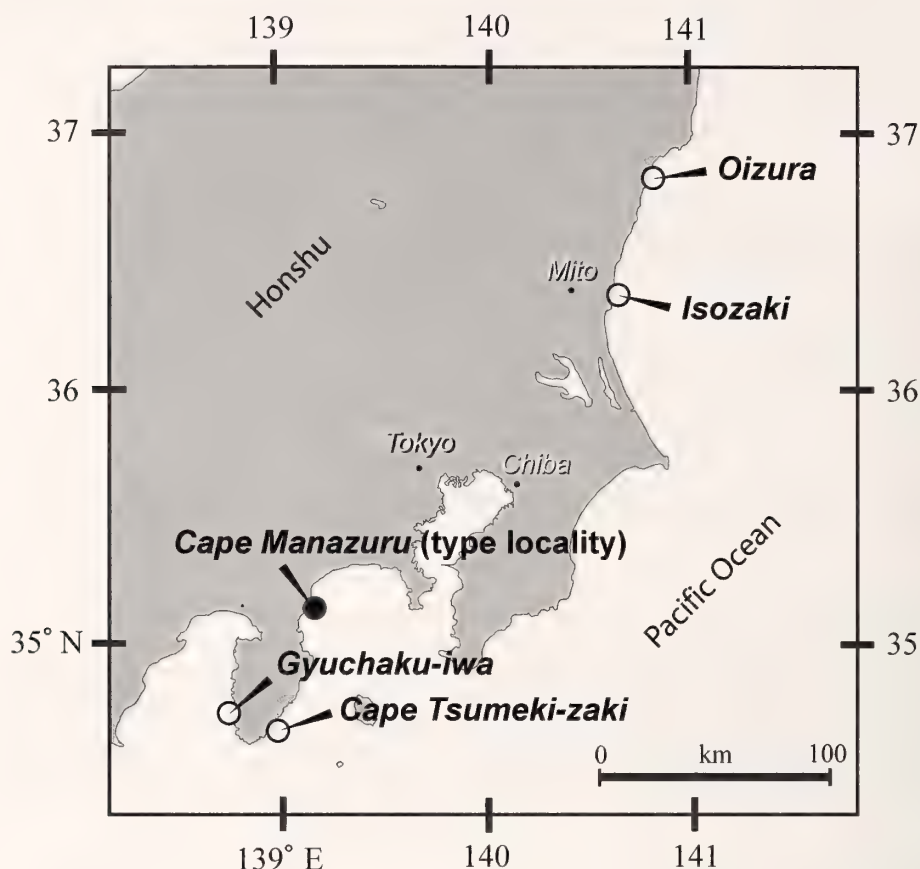


Figure 1. Localities of *Nipponolimopsis littoralis* n. sp.

solution, fixed with 10% neutralized sea water-diluted formalin for at least 3 days, rinsed in tap water for one hour, then preserved in 70% ethanol. The shells were dissolved by immersing in a diluted solution of HCl for several minutes, and dissected under a binocular microscope. Three samples were stained with eosin or toluidine blue for at least 30 min to evaluate tissue types. For taxonomic comparison, the type specimens described by Yokoyama (1910, 1922) were reinvestigated and photographed, since details were not given sufficiently in the original descriptions. The data from other species were reviewed and compiled from literature. The type specimens of new species are deposited in The University Museum, The University of Tokyo (UMUT) and the National Science Museum, Tokyo (NSMT).

SYSTEMATICS

Superfamily Limopsoidea Dall, 1895

Family Limopsidae Dall, 1895

Genus *Nipponolimopsis* Habe, 1951

Type species: *Limopsis nipponica* Yokoyama, 1922

(original designation) = *Cyrella decussata* A. Adams, 1862

Diagnosis: Shell small (less than 14 mm); surface finely and regularly reticulate; periostracum thick, densely hairy; anterior area of shell shorter than posterior; anterior arc of hinge teeth four or fewer in number, nearly vertical to hinge line; posterior arc of hinge teeth seven or fewer, oblique or subparallel to hinge line; anterior adductor muscle scar notably reduced in size below anteriormost hinge tooth; posterior adductor muscle scar much larger than anterior, remote from dorsal margin; inner ventral margin lacking crenulations.

Remarks: Following the majority of authors (e.g., Newell, 1969; Kuroda et al., 1971; Habe, 1977; Tevesz, 1977; Coan et al., 2000; Matsukuma, 2000), we tentatively allocate *Nipponolimopsis* to the Limopsidae rather than the Philobryidae. This treatment is mainly based on the presence of typical limopsid characters such as a finely reticulate sculpture, a thick hairy periostracum, prominent taxodont hinges both at the anterior and posterior sides. Oliver (1981:71) regarded the genus as a member of the Philobryidae, putting an



Figure 2. Habitat of *Nipponolimopsis littoralis* n. sp. in type locality. Arrow indicates approximate position where holotype was collected.

emphasis on a cap-shaped prodissococonch. The retention of the byssus at the adult stage, small size, and brooding habit may also support its closeness to philobryid members. The shell morphology of philobryids is highly variable in the hinge teeth, ligament, sculpture, and muscle scar (see Tevesz, 1977 for details), and the family might be a polyphyletic grade due to miniaturization and brooding, rather than a clade. Family-level systematics (cf. Oliver & Holmes, 2006: table 1) must be revised through phylogenetic analysis of all members of Limopsoidea.

Nipponolimopsis littoralis Sasaki & Haga n.sp.

(Figures 3–6)

Material: Holotype (2.0 mm in height, 1.6 mm in length, UMUT RM29331: Figure 3A), paratype #1 (UMUT RM29332: Figure 3B), paratype #2 (UMUT RM29333: Figure 3C–D): Cape Manazuru, Kanagawa Prefecture, Japan, July 21, 2005, collected by T. Sasaki; 3 paratypes (UMUT RM29334–29336); Oizura, Kitai-

baraki, Ibaraki Prefecture, Japan, July 9, 2002, collected by T. Haga; 9 paratypes (UMUT RM29337–29345): Isozaki, Hitachinaka, Ibaraki Prefecture, Japan, May 5, 2003, collected by T. Haga; 4 paratypes (UMUT RM29346–29349): Cape Tsumekizaki, Shimoda, Shizuoka Prefecture, Japan, May 8, 2005, collected by T. Haga; 2 paratypes, dead disarticulate valves from the subtidal zone, Gyuchaku-iwa, Kumomi, Matsuzaki, Shizuoka Prefecture, Japan, collected by Mr. Hisanao Nabeshima in 1990s (NSMT Mo73813, 73814).

Diagnosis: Shell height smaller than 3 mm; periostracum composed of radially arranged thick bristles and thin commarginally lamellate membranes; obliquely oval outline without prominent ventral extension; cancellate sculpture consisting of thicker radial ribs and thinner commarginal ridges; prodissococonch with weak collar-like marginal ridge, finely pitted sculpture, and deep umbonal depression; hinge teeth three in anterior and four in posterior row.

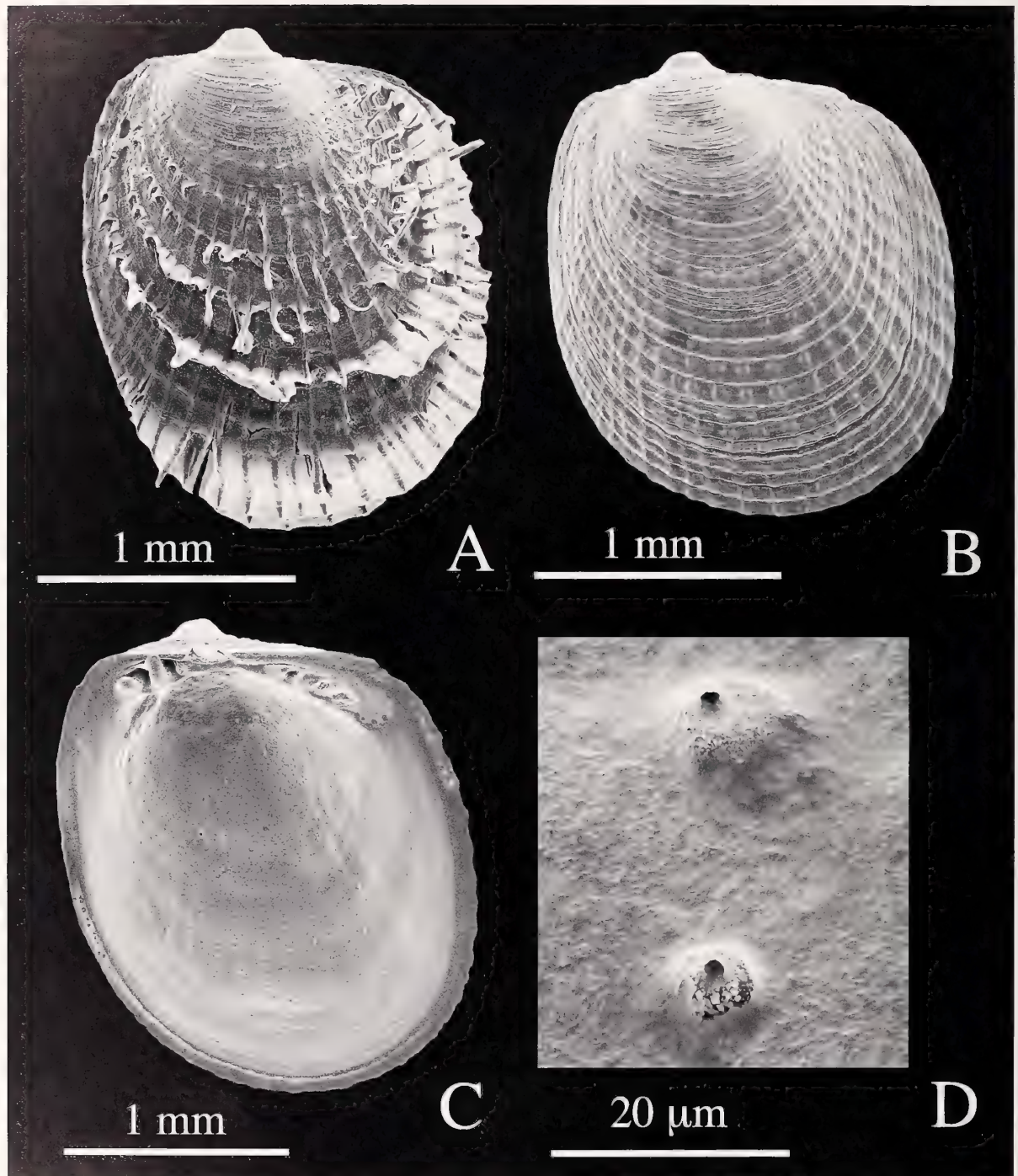


Figure 3. *Nipponolimopsis littoralis* n. sp. A. Holotype with complete periostracum. UMUT RM29333. B. Paratype #1 with periostracum artificially removed. UMUT RM29332. C. Inner view of paratype #2. UMUT RM29333. D. Enlarged view of shell pores on shell interior of paratype #2.

Shell: The shell is small for the family, subquadrate, inequilateral, and equivalve. The dorsal margin is straight. The anterior and posterior margins are almost parallel, slightly convex, roundly continuous with

a smoothly convex ventral margin. The umbo is located at 39% of the hinge line anteriorly (Figure 3), orthogyrate and projected dorsally. The periostracum consists of two elements (Figure 3A): (1) Sparse

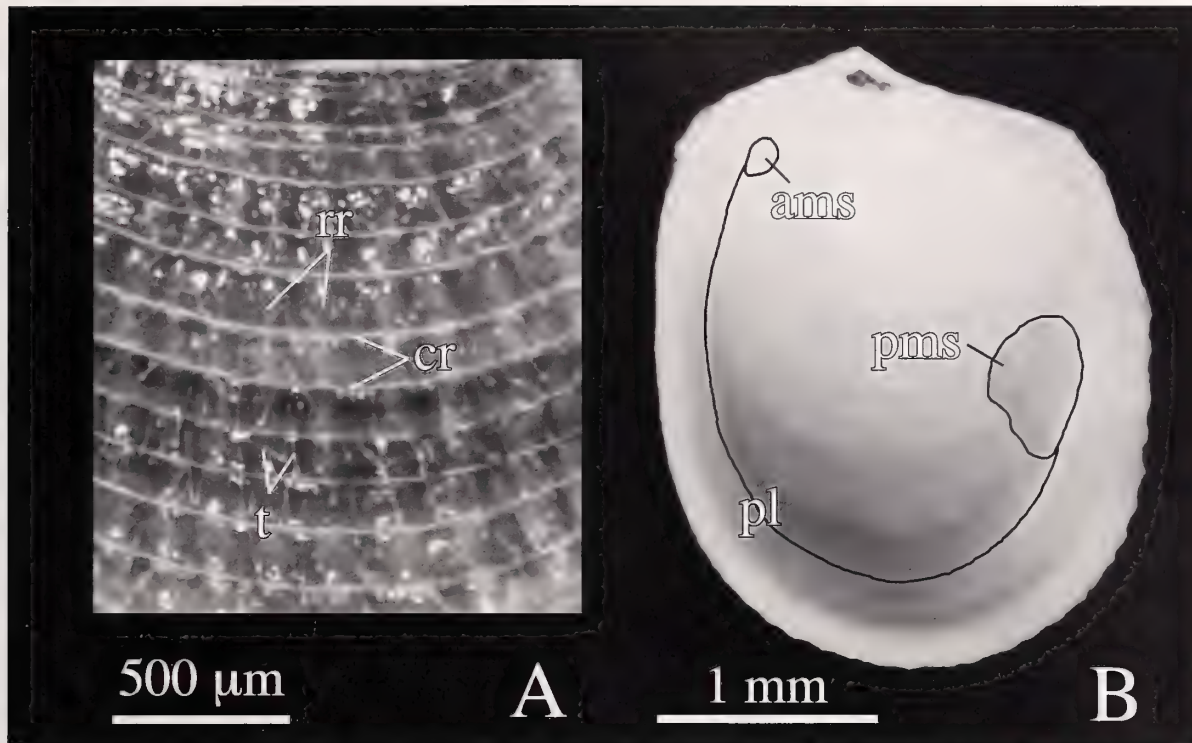


Figure 4. *Nipponolimopsis littoralis* n. sp. A. Enlarged view of outer surface after periostracum artificially dissolved. B. Inner view of shell showing position of muscle scars and pallial line. Paratype UMUT RM29334. Abbreviations: ams = anterior adductor muscle scar, cr = commarginal ridge, pl = pallial line, pms = posterior adductor muscle scar, rr = radial rib, t = tubule seen through shell.

periostracal bristles are arranged radially and project periodically along commarginal lines. (2) A thin filmy periostracum covers the entire shell surface and also connects periostracal bristles to form commarginal lamellate membranes. In gerontic specimens, the latter element of the periostracum is more easily worn away than the former. The outer surface of the shell is sculptured by ca. 30–40 radial ribs (rr) and also sharp commarginal ridges (cr: Figure 4A). When the periostracum is removed, microscopic tubules are visible as fine lines seen through the shell (t: Figure 4A; cf. Reindl & Haszprunar, 1996 for internal structure). The prodissoconch is discoidal in outline, 340 μm in length (Figure 5A), finely pitted on the surface (Figure 5B) and marked with a conspicuous depression (Figure 5C). The margin of the prodissoconch is thickened (Figure 5A). The hinge plate is straight dorsally, arcuate ventrally, and the thinnest below the umbo (Figure 5C). The hinge teeth are taxodont and consist of three anterior and four posterior teeth (Figure 5D). The teeth and sockets form a larger angle to the hinge axis at the anterior arc than the posterior; the posteriormost tooth is nearly parallel to the hinge axis. The ligament is alivincular, dorsally external; the resilium is small and triangular (Figure 5C). The cardinal area is

narrow and striated by fine vertical ridges. The inner surface of the shell is smooth except for microscopic pores (Figure 3D). The anterior adductor muscle scar (ams) is much smaller than the posterior (pms: Figure 4B). The pallial line (pl: Figure 4B) is nearly parallel to the shell margin. The inner margin is thickened with a commarginal ridge and smooth.

Muscular system: The animal is heteromyarian with a vestigial anterior adductor muscle (aam: Figure 6A) and a larger posterior adductor muscle (pam). Unlike most limopsids, an anterior pedal retractor muscle is absent. A small pedal protractor muscle (ppm) inserts beneath the anterior adductor muscle. The posterior adductor muscle is flanked by a well-developed posterior retractor muscle (prm) from which the byssal retractor element (bre) is independently branched out. The anterior part of the posterior retractor muscles covers most of the visceral mass.

Mantle and pallial eyes: Each mantle margin lacks pallial tentacles and comprises the outer, middle, and inner folds. A transparent periostracum protrudes from an incision between the outer and middle folds. Mantle fusion occurs only on both sides of a taxodont hinge, and there are no inhalant and exhalant apertures on the

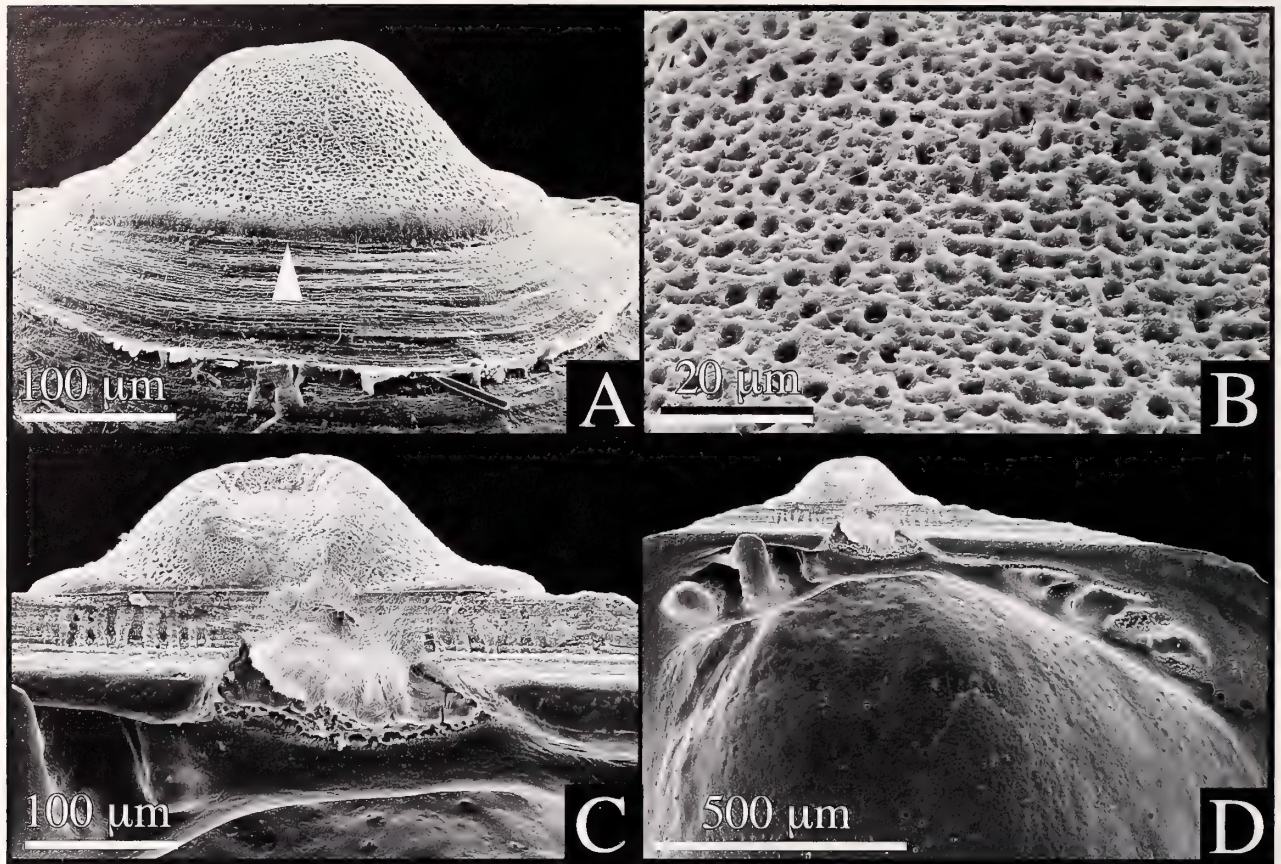
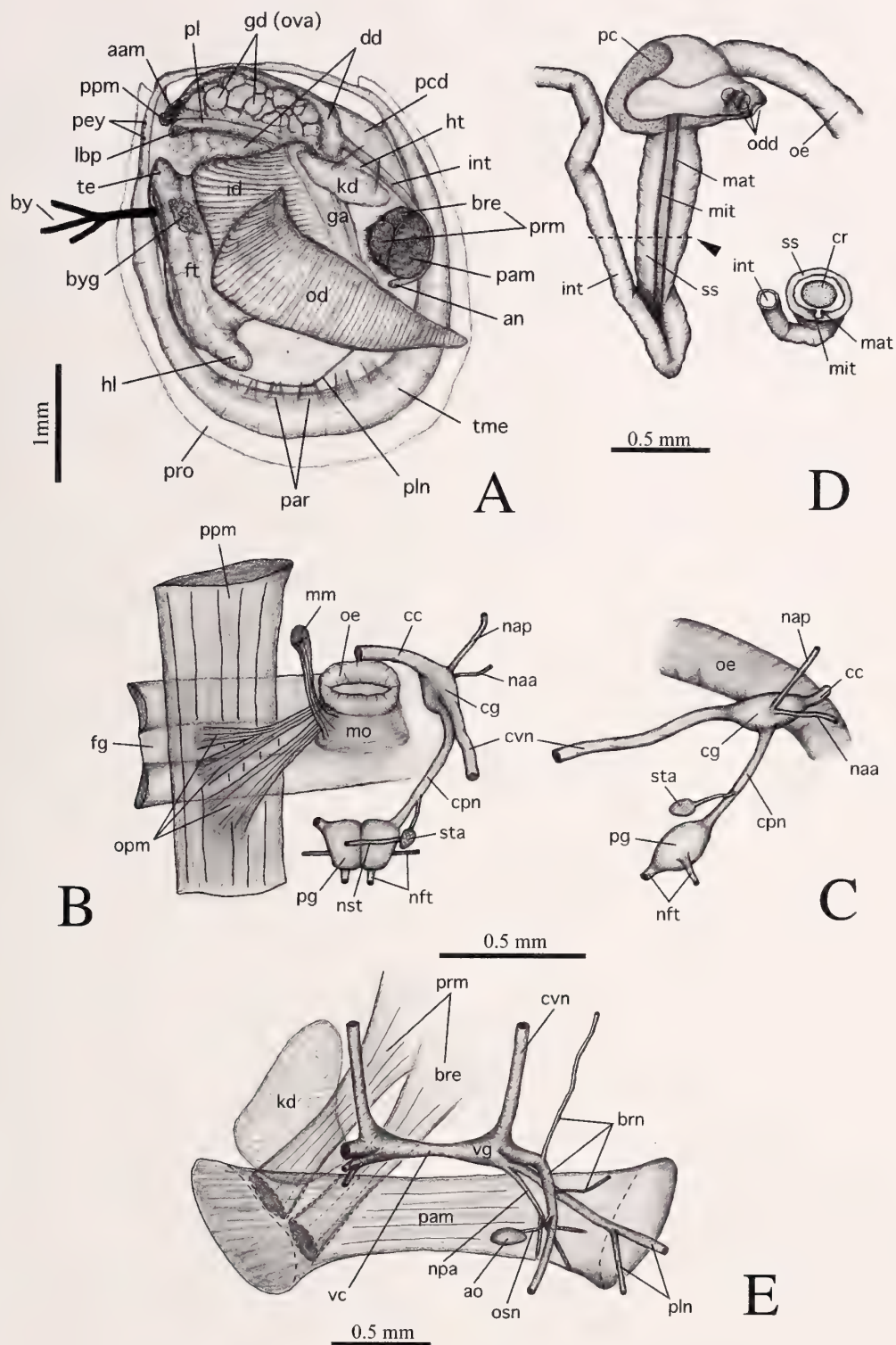


Figure 5. *Nipponolimopsis littoralis* n. sp. A. Prodissoconch of holotype. Arrowhead indicates boundary between prodissoconch and dissoconch. B. Enlarged view of prodissoconch sculpture. C. Hinge and umbonal part of paratype #2 (UMUT RM29333). D. Enlarged view of hinge teeth.

posterior mantle edge. The mantle margin is thickened (tme: Figure 6A) and few concentric muscle fibers are seen through it. The bundles of the pallial retractor muscle (par) are located on the inner side of a thickened mantle edge. They are innervated by the pallial nerves (pln) originating from the visceral ganglia (vg) via the

ventral part of the posterior adductor muscle. White granules, possibly mucous glands, are present on the inner side of each mantle wall close to the posterior end of the gill axes. In a narrow area of the outer fold, there are two to five brown-pigmented eyespots (pallial eyes; pey: Figure 6A) beneath the periostracum.

Figure 6. *Nipponolimopsis littoralis* n. sp. A. Left lateral view of animal with left valve and mantle removed. B. Anterior view of mouth, associated muscles, and circum-esophageal nervous system. C. Right lateral view of digestive tract. Arrowhead indicates position of cross section which is shown on right side of figure. D. Posterior adductor muscle and adjacent nervous system seen from posterior side. Abbreviations: aam = anterior adductor muscle, an = anus, ao = abdominal organ, bre = byssal retractor element of posterior retractor muscle, brn = branchial nerve, byg = byssus groove, cc = cerebral commissure, cg = cerebral ganglion, cpn = cerebropedal nerve, cr = crystalline style, cvn = cerebrovisceral nerve, dd = digestive diverticulum, fg = food groove, ft = foot, ga = gill axis, hl = heel of foot, ht = heart, id = inner demibranch, int = intestine, kd = kidney, lbp = labial palp, mat = major typhlosole, mit = minor typhlosole, mm = muscular fiber supporting mouth, mo = mouth, naa = nerve to anterior adductor muscle, nap = nerve to anterior part of pallial line, nft = nerve to foot, npa = nerve to posterior adductor muscle, nst = nerve connecting statocysts, od = outer demibranch, odd = opening into digestive diverticulum, oe = esophagus, opm = muscular fiber originated from pedal protractor muscle, pam = posterior adductor muscle, par = pallial retractor muscle, pc = pigmented cell, pcd = pericardium, pey = pallial eyes, pg = pedal ganglion, pl = palps, pln = pallial nerve, ppm = pedal protractor muscle, prn = posterior retractor muscle, prm = posterior retractor muscle, ss = style sac, sta = statocyst, te = toe of foot, tme = thickened mantle margin, vc = visceral commissure, vg = visceral ganglion.



Foot: The foot is large, highly muscular, and laterally compressed with two terminal projections termed the toe (te) and the heel (hl: Figure 6A). On the ventral surface, there is a deep byssal slit anteriorly and a long but shallow byssal groove posteriorly. A relatively large byssal gland (byg) is visible in orange in living animals at the base of the mid-anterior region. The byssal threads are translucent, thin, slightly grayish.

Ctenidia and labial palps: The ctenidia are filibranchiate and consist of the outer (od) and inner demibranchs (id). The outer demibranchs are significantly smaller than the inner demibranchs. The anterior pallial space in front of the outer demibranchs is used to brood larvae. The posterior one-third of the outer demibranch is free from the visceral mass and highly mobile. When the animals are alive, the posterior tips of the ctenidia project beyond the shell edge.

Dorsally situated food grooves (fg: fig. 5B) are surrounded by the palps (pl) extended from the anterior ends of muscular gill axes (ga), and finally terminate as a laterally inflated, slit-like mouth. Small labial palps (lbp) are thick, triangular and corrugated with approximately five sorting grooves.

Digestive system: A slit-like mouth (mo) is located between the pedal protractor muscles (ppm) and well-developed food grooves. The ventral part of the mouth is supported by two muscular fibers (mm: Figure 6B). From this simple orifice, a long, slightly dorso-ventrally flattened oesophagus (oe) arises and is laterally supported by muscular fibers (opm: Figure 6B) originating from the wall of the visceral mass.

The stomach is mushroom-shaped and comprises two parts, *viz.* the dorsal chamber and the ventral tract. The anterior part of the dorsal chamber is connected to yellowish-gray digestive diverticula (dd) with two or three openings (odd) on the right side and one on the left. The digestive diverticula surround most of the stomach and spread into part of the oesophagus, but do not enter into the foot. The postero-ventral surface of the stomach bears bright brown-pigmented cells (pc: Figure 6D), and food tracts are traceable along a transparent area on the right stomach wall. These tracts fuse with the major and minor typhlosoles (mat, mit: Figure 6B) on the right side at the base of the style sac (ss). The major and minor typhlosoles are nearly equal in thickness, though the former is slightly stouter than the latter. The crystalline style (cr) is transparent, cylindrical and laterally flattened. The dorsal tip of the crystalline style in contact with the gastric shield is small and needle-shaped. Detailed inner morphology of the stomach was not observed.

The intestine (int) is long and ascends from the ventral right side of the style sac to the same level as the dorsal portion of the stomach, and finally turns in

a posterior direction. The intestine penetrates the heart and terminates as a simple anus (an: Figure 6A) below the middle portion of the posterior adductor muscle.

Vascular and excretory systems: The pericardium (pcd: Figure 6A) occupies the postero-dorsal portion of the visceral mass. The heart (ht) is almost transparent, membranous, and consists of the ventricle and laterally paired auricles. The ventricle is penetrated by the intestine.

The kidney (kd: Figure 6A) is large, translucent, membranous and comprising two components positioned laterally below the heart. The kidney ducts are significantly short and directly open into the supra-branchial cavity.

Reproductive system: Sexes are separate. The gonads (gd: Figure 6A) are distributed above the stomach and oesophagus, and extend towards the pedal ganglia along the wall of the visceral mass. The ovary and testis are both whitish, however, the former is distinguished from the latter by spherical shape and large size. The gonoducts were not observed in this study.

Nervous system: The cerebral ganglia are positioned lateral to the oesophagus. The pedal ganglia are embedded in the anterior portion of the foot. The visceral ganglia are located antero-ventral to the posterior adductor muscle.

The cerebral ganglia (cg: Figure 6B–C) are slender, cylindrical, and closely lateral to the anterior portion of the oesophagus. The cerebral commissure (cc) connects each cerebral ganglion beneath the oesophagus. Two small nerves ascend from the lateral surface of each ganglion: the ventral one is extended to the anterior portion of the pallial line (nap: Figure 6B–C) and another is to the anterior adductor muscle (naa). The pedal ganglia (pg: Figure 6B–C) are trapezoid, nearly equal in size to the cerebral ganglia, located at the anterior base of the foot, and connected to the cerebral ganglia with short cerebropedal nerves (cpn: Figure 6B–C). Since they are fused together, there is no commissure between them. From the pedal ganglia, two branches of small nerves are sent laterally and ventrally to the foot region (nft: Figure 6B–C). The statocysts (sta) are tiny, brownish, embedded in connective tissues on the wall of the visceral mass, and connected with the cerebropedal nerves and with each other by a small transverse commissure (nst). The inside of the statocysts were not observed in this study.

The cerebrovisceral nerves (cvn: Figure 6B–C) connect the cerebral and visceral ganglia. Large, dorso-ventrally flattened visceral ganglia (vg: Figure 6E) and their adjacent nerves form the most complicated part in the nervous system. The visceral ganglia are situated between the posterior end of the visceral mass and the posterior adductor muscle, and each ganglion is linked

with a thick and short visceral commissure (vc: Figure 6E). The visceral ganglia emit three nerves, viz. the branchial nerves (brn), the pallial nerves (pln), and nerves to the posterior adductor muscle. The branchial nerves are the most prominent element arising from the visceral ganglia, and the main thick nerves innervate the ctenidia along the muscular gill axes. The osphradial nerves (osn) are separated from the main ctenidial nerves and innervate the abdominal sense organ (ao) lying on either side of the anus. The pallial nerves (pln) are derived from the visceral ganglia dividing into two offshoots below the lateral margin of the posterior adductor muscle, descend along thickened mantle edges (tme), and finally reach the bundles of the mantle retractor muscles. The nerves to the posterior adductor muscle (npa: Figure 6E) bear three offshoots but they all terminate after a short distance.

Type locality: Cape Manazuru, Kanagawa Prefecture, Japan (35°08'35"N, 139°09'42"E) (Figures 1, 2).

Distribution: Pacific coasts of central Japanese mainland from Izu Peninsula to Ibaraki Prefecture.

Habitat: The new species byssally attaches to the undersides of partly buried, stable boulders in the upper to lower intertidal zone of open coasts exposed to waves.

Etymology: The species epithet is derived from the intertidal habitat of the species. The Latin word "*littoralis*" means "of the seashore."

Nipponolimopsis decussata (A. Adams, 1862)

Cyrella decussata A. Adams, 1862: p. 295.

Limopsis nipponica Yokoyama, 1922: p. 195, pl. 17, figs. 16–17.

Limopsis skinshitai Kuroda, 1930: p. 18, figs. 24–25.

Limopsis hilgendorfi Thiele in Thiele & Jaeckel, 1931: pl. 6, figs. 21, 21a.

Nipponolimopsis nipponica: Habe, 1951: p. 45, figs. 83–84.

Aspalima (*Nipponolimopsis*) *decussata*: Habe, 1953: p. 206, pl. 29, figs. 20–21; Habe, 1961a: p. 112, pl. 50, fig. 7.

Limopsis (*Nipponolimopsis*) *nipponica*: Taki & Oyama, 1954: pl. 37, figs. 16–17 (reproduction of Yokoyama, 1922); Oyama, 1973: p. 76, pl. 21, figs. 21–22 (reproduction of Yokoyama, 1922).

Nipponolimopsis decussata: Kuroda et al., 1971: pp. 340–341, pl. 117, fig. 15; Habe, 1977: p. 50, pl. 9, figs. 4–5; Oliver, 1981: p. 67, figs. 11–12; Coan et al., 2000: p. 148–149, pl. 21; Matsukuma, 2000: pp. 856–857, pl. 426.

Diagnosis: Shell height 5 mm or smaller; anterodorsal margin truncate; posterior margin more roundly and

widely convex than anterior; hinge teeth three in anterior, four in posterior; hinge line and anterior margin variable, forming nearly right angle.

Type specimen: Unknown.

Type locality: Gotto Islands, 48 fathoms (= Goto Islands, northwestern Kyushu, Japan).

Distribution: Pleistocene: Kioroshi Formation, Kioroshi, Chiba, Japan (Yokoyama, 1922 as *Limopsis nipponica*). Recent: Indonesia (Thiele & Jaeckel, 1931 as *Limopsis hilgendorfi*); Iwate Prefecture to East China Sea, Sea of Japan, 40–400 m (Higo et al., 1997: 428, B262); southeastern Hokkaido to Kyushu, 50–100 m (Matsukuma, 2000:857); western Aleutian Islands, Alaska, 219–388 m (Coan et al., 2000:148).

Remarks: Although there are multiple problems concerning the true identity of this species, it is currently most practical to follow the conventional interpretation by Dr. Kuroda and Dr. Habe to avoid confusion. (1) The identify of this species is not unambiguous, because an unfigured type of Adams (1862) is missing (cf. Makiyama, 1929; Kuroda & Habe, 1954; Habe, 1961b, 1985; Higo et al., 2001 for types of *A. Adams*). Finding Adams's specimen is the most important thing in revising this species. (2) *Limopsis hildendorfi* Thiele & Jaeckel, 1931 and "*N. decussata*" from outside of temperate Japanese waters may not belong to the same conspecific population, but this needs further investigation. (3) It is also possible that *Limopsis nipponica* Yokoyama, 1922 (Figure 7: lectotype) represents an independent extinct species, since it is more obliquely elongate than Recent specimens of *N. decussata* (and also than *N. littoralis*). (4) The holotype of *Limopsis skinshitai* Kuroda, 1930 is missing (see Hanshin Shell Club, 1986; Kikuchi et al., 1996 for types of Kuroda).

Nipponolimopsis azumana (Yokoyama, 1910)

(Figure 8)

Limopsis azumata Yokoyama, 1910: p. 3, pl. 9, figs. 16–18; Yokoyama, 1920: p. 174–175, pl. 18, figs. 19–21. *Limopsis truncata* Yokoyama, 1910: p. 4, pl. 9, figs. 13–14.

Aspalima (*Nipponolimopsis*) *azumana*: Habe, 1953: p. 207, pl. 29, fig. 22–23.

Limopsis (*Nipponolimopsis*) *azumana*: Taki & Oyama, 1954: pl. 19, figs. 19–21 (reproduction of Yokoyama, 1920); Oyama, 1973: p. 76, pl. 21, figs. 12, 15, 19 (reproduction of Yokoyama, 1920).

Nipponolimopsis azumana: Kuroda et al., 1971: p. 341, pl. 71, figs. 21–22; Itoigawa et al., 1974: pp. 59–60, pl. 7, fig. 2; Itoigawa et al., 1981: pl. 4, fig. 3; Matsukuma, 2000: pp. 856–858, pl. 426; Ogasawara, 2001: p. 303.

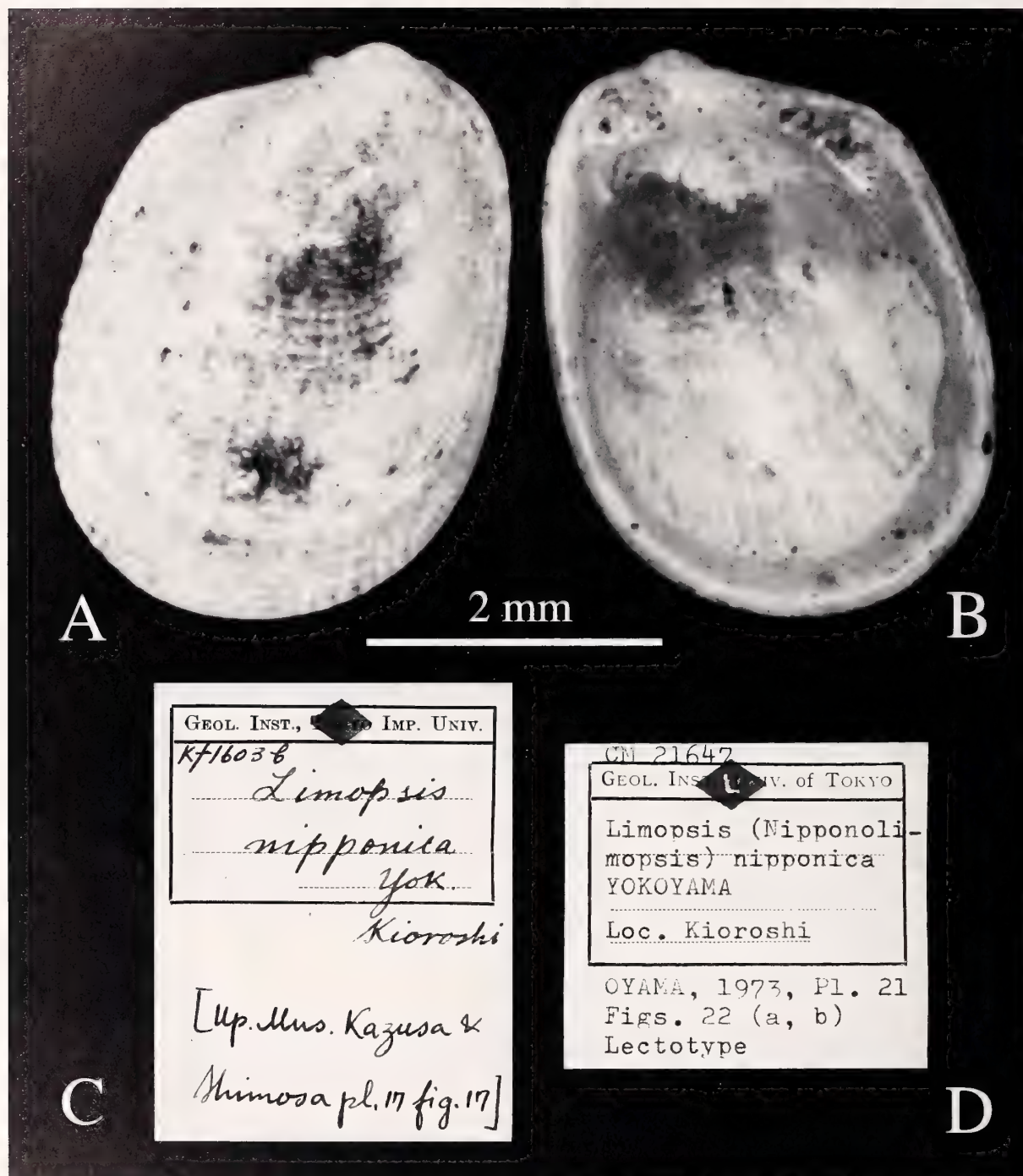


Figure 7. Lectotype of *Limopsis nipponica* Yokoyama, 1922. UMUT CM21647. A. Exterior. B. Interior. C–D. Labels attached to lectotype.

Limopsis (*Limopsis*) *azumana*: Tanabe, 1990: p. 637, fig. 3.

Diagnosis: Shell large for genus, 14 mm or less in height, markedly widened anteroventrally; posterior

margin markedly truncated, straight; anterior hinge teeth four in number, nearly vertical to hinge line; posterior hinge teeth seven, oblique to hinge line; anterior margin and hinge line forming right angle.

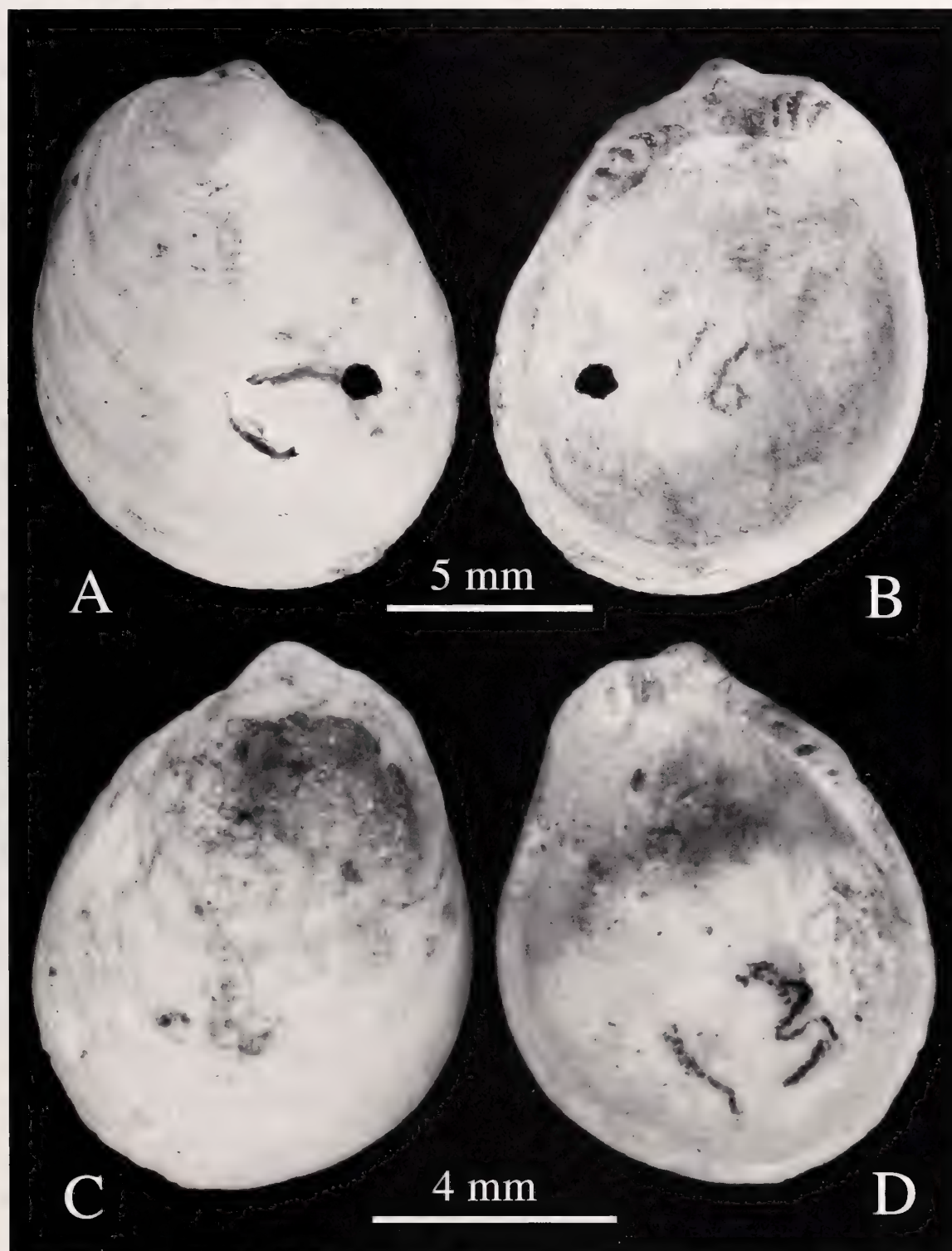


Figure 8. *Nipponolimopsis azumana* (Yokoyama, 1910). A–B. *Limopsis azumana* Yokoyama, 1910. One of syntypes here designated as lectotype. UMUT CM26403. C–D. *Limopsis truncata* Yokoyama, 1910. One of syntypes here designated as lectotype. UMUT CM26404.

Type specimen: Lectotype UMUT CM26403 (Figure 8A, B). See Appendix for paralectotypes.

Type locality: Koshiba (= Sea cliff of Shiba, Kanazawa-machi, Yokohama, Kanagawa Prefecture, Japan; 35°20'05"N, 139°38'06"E), Pleistocene.

Distribution: Miocene: Mizunami Group, Mizunami, Gifu, Japan (Itoigawa et al., 1974, 1981). Pleistocene: Koshiba Formation, Yokoyama, Kanagawa, Japan (Yokoyama, 1910, 1920), Lower Shimoda Formation, Ninomiya, Kanagawa, Japan (Tanabe, 1990). Recent: Sagami Bay to Kii Peninsula, 100–250 m (Higo et al., 1999:428, B263; Matsukuma, 2000:857).

Remarks: The type specimens of *Limopsis azumata* Yokoyama, 1910 and *Limopsis truncata* Yokoyama, 1910 had never been critically revised since their original description. We designate lectotypes of these two nominal species and illustrate them in Figure 8 to clearly define their identity. The surface of both lectotypes is smoothened by erosion.

Nipponolimopsis kutekenensis Noda, 1980

Nipponolimopsis kutekenensis Noda, 1980: pp. 78–79, pl. 12, fig. 11a, b; Ogasawara, 2001: 303.

Diagnosis: Shell extended anteroventrally; surface reticulate, roughened by dense concentric ribs; hinge teeth four in anterior, seven in posterior; angle between anterior margin and hinge line larger than 90°.

Type specimen: Holotype IGUT10338 (Institute of Geoscience, University of Tsukuba).

Type locality: Shinzato Formation, Chinen, Okinawa, Japan, Pliocene.

Distribution: Known only from the type locality.

Remarks: The species is most similar to *N. azumana* but different in having prominent concentric ribs and larger angle between the anterior margin and the hinge line (greater than 90°) (Noda, 1980: 78–79, pl. 12, fig. 11a, b).

Nipponolimopsis sp.

(Figure 9)

Shell: The outline is somewhat square (Figure 9A); the dorsal margin completely straight; the anterior margin at the right angle to the dorsal margin; the posterior margin is straight and oblique; the ventral margin is weakly convex. The surface is sculptured by conspicuous reticulate sculpture (Figure 9B). The number of the hinge teeth is four in the anterior and five in the posterior (Figure 9C). The prodissococonch at the beak is semicircular and fringed by an extremely thick ridge

(mr: Figure 9D); the initial center of the prodissococonch is also strongly ridged (cr: Figure 9D).

Locality: Off Tanabe, Wakayama Prefecture, Japan (R/V *Tansei-Maru*, cruise KT-05-30, station TN1(1), 33°39.05'N, 135°09.89'E–33°38.96'N, 135°10.16'E, 170.3–173.1 m deep).

Remarks: This species is different from any known members of *Nipponolimopsis* in its subsquare outline. The prodissococonch is characteristically margined by a conspicuous ridge in clear contrast to that of *N. littoralis* (Figure 5). This is probably another new species, but we obtained only a single dead valve so far.

DISCUSSION

The new species is allocated to the genus *Nipponolimopsis* Habe, 1951 based on the combination of several characters such as (1) a small adult size, (2) a reticulate sculpture, (3) a thick periostracum, (4) an anteriorly positioned umbo, (5) a simple alivincular ligament (type C of Oliver, 1981), (6) a small number of taxodont hinge teeth (three anterior and four posterior teeth), (7) the anterior hinge teeth forming larger angles to the hinge axis than inclined posterior teeth, (8) the presence of the marginal locking groove along the inner ventral margin (cf. Oliver, 1981:fig. 12), and (9) a large prodissococonch associated with brooding habit (see Malchus & Warén, 2005 for prodissococonchs of various limopsids for comparison). In the original diagnosis, Habe (1951, 1977:49) mentioned a crenulated inner shell margin. However, such a character state is not confirmed in any species he assigned to the genus, and therefore, it is regarded as an erroneous observation.

By comparison with other described species, *N. littoralis* is diagnosed by four conchological characters. (1) The periostracum is the most distinctive character of the new species. It consists of sparsely and radially arranged, erected bristles and commarginally lamellate membranes. The periostracum of *N. decussata* (Habe, 1961a: pl. 50, fig. 7) and *N. azumana* (Kuroda et al., 1971: pl. 71, fig. 22; Matsukuma, 2000:856) is uniformly hairy and densely covers the shell surface. (2) The outline of the shell of *N. littoralis* is similar to that of *N. decussata* and *N. kutekenensis*, but distinguished from that of *N. azumana* which is more ventrally widened than dorsally (Figure 7). (3) The sculpture of the exterior is similarly reticulate in *N. littoralis*, *N. decussata*, and *N. azumana* (Matsukuma, 2000:856), but concentrically sharpened in *N. kutekenensis* (Noda, 1980: pl. 12, fig. 11a, b). (4) The prodissococonch of *N. littoralis* is characterized by a weak marginal ridge, a finely pitted sculpture, and a deep depression at the beak (Figure 4). This morphology is clearly in contrast to a smooth and rounded prodissococonch of *N. azumana* (Tanabe, 1990) and a more

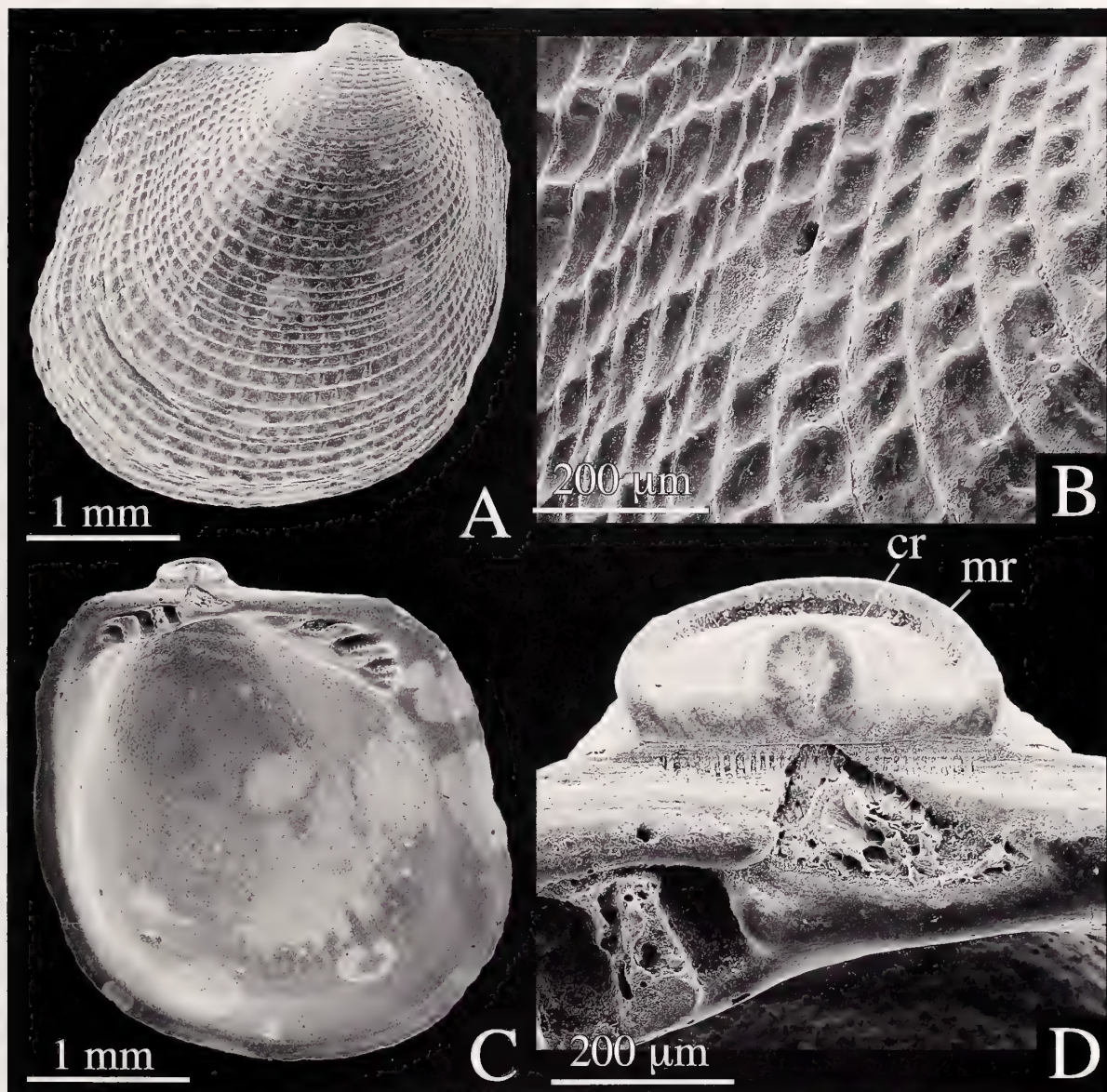


Figure 9. *Nipponolimopsis* sp. A. Shell exterior. B. Enlarged view of exterior sculpture. C. Shell interior. D. Enlarged view of prodissococonch. Disarticulated right valve from sediments dredged from off Tanabe, Wakayama Prefecture, Japan, w170.3–173.1 m deep. UMUT RM29350. Abbreviations: cr = central ridge, mr = marginal ridge.

depressed prodissococonch of *N. decussata* (Oliver, 1981:fig. 12). An unidentified species of *Nipponolimopsis* (Figure 9) also possesses a strikingly different prodissococonch with a sharply ridged fringe and a narrower depression. In addition to these differences in morphology, the new species is also separated by bathymetric distribution. The habitats of *N. decussata* and *N. azumana* range from 50 to 100 m and from 100 to 250 m, respectively (Matsukuma, 2000:857), while *N. littoralis* is confined to the intertidal zone.

At present, it is entirely uncertain whether anatomical characters are useful in diagnosing species, because

no comparable observations have been carried out for the genus. Compared to other limopsids, the ctenidia of *N. littoralis* are different in that the outer demibranchs are smaller than the inner demibranchs at the anterior side (Figure 5A). This morphology is functionally related to the brooding habit of the species. The anterior space of the pallial cavity where the outer demibranchs are lacking is used to brood eggs and larvae. The reduction of the anterior side, especially in the anterior adductor muscle, seems to be correlated with an epibyssate mode of life, as is found in other members of the Limopsidae (Oliver, 1981).

The habitat of the new species on the intertidal bolder shores is exceptional and noteworthy for *Nipponolimopsis*. Other extant species of the genus dwell in the lower subtidal zone (e.g., Oliver & Allen, 1980; Oliver, 1981; Coan et al., 2000; Matsukuma, 2000) and no member has been recorded from the intertidal rocky shores. In the family Philobryidae, most species are recorded from the shallow subtidal zone (Tevesz, 1977; Powell, 1979; Lamprell & Healy, 1998; Coan et al., 2000; Malchus, 2006), but their microhabitats are unknown except for the records from brown or red algae (Tevesz, 1977:30), sea-urchin spines (Janssen, 1997), undersides of stones (Morton, 1978), and submarine caves (Hayami & Kase, 1993). By contrast, *N. littoralis* dwells in the intertidal zone, hanging on the undersides of partly buried, stable boulders in wave-exposed coasts. In the localities (Figure 1), the same habitat is shared only with a limited number of bivalves (e.g., *Ostrea subucula* and *Porterius dalli*).

No ecological and developmental observations have been made on *Nipponolimopsis*. We confirmed that *N. littoralis* broods the larvae with fully developed prodissoconchs in the pallial cavity. This fact indicates lecithotrophic benthic development of this species without a planktonic stage. Tanabe (1990) inferred that *N. azumana* probably undergoes direct development or ovoviviparity based on the morphology and size of well-preserved prodissoconchs of juvenile fossil specimens. Our observation on an unidentified species of *Nipponolimopsis* (Figure 8) also shows a large prodissoconch I (410 µm in length) without the formation of a prodissoconch II. Thus, the small adult size, a relatively large prodissoconch, brooding habit, and benthic development without a planktonic stage, might be a set of shared characters of the members of *Nipponolimopsis*. More detailed comparison on reproduction and development is necessary to evaluate these characters in future studies.

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APPENDIX

Registration number, references, and present status of *Nipponolimopsis* specimens described by Yokoyama (1910, 1920, 1922).

Limopsis nipponica Yokoyama, 1922: UMUT CM21647: Yokoyama, 1922: p. 195, pl. 17, fig. 17 (as syntype); Taki & Oyama, 1954: pl. 37, fig. 17 (designated as holotype [to be lectotype]); Oyama, 1973: p. 76, pl. 21, fig. 22a, b (as lectotype). Present status: Lectotype, present in UMUT (Figure 5). UMUT CM21646: Yokoyama, 1922: p. 195, pl. 17, fig. 16 (as syntype); Taki & Oyama, 1954: pl. 37, fig. 16 (designated as paratype [to be Paralectotype]); Oyama, 1973: p. 76, pl. 21, fig. 21. Present status: Paralectotype, present in UMUT. UMUT CM21648: Yokoyama, 1922: p. 195, not figured (as syntype). Present status: Paralectotype, present in UMUT. UMUT CM21649: Yokoyama, 1922: p. 195, not figured (as syntype). Present status: Paralectotype, present in UMUT.

Limopsis azumana Yokoyama, 1910: UMUT CM24526: Yokoyama, 1910: p. 3, pl. 9, fig. 17 (as syntype). Present status: Paralectotype designated in this study, missing. UMUT CM26402: Yokoyama, 1910: p. 3, pl. 9, fig. 16 (as syntype). Present status: Paralectotype designated in this study, present in UMUT (Figure 6A, B). UMUT CM26403: Yokoyama, 1910: p. 3, pl. 9, fig. 18 (as syntype). Present status: Lectotype designated in this study, present in UMUT (Figure 6A, B). UMUT CM24544: Yokoyama, 1920: p. 174, pl. 18, fig. 19a–c; Taki and Oyama, 1954: pl. 19, fig. 19; Oyama, 1973: p. 76, pl. 21, fig. 12a–c (as paratype: error). Present status: Figured non-type specimen, missing. UMUT CM24545: Yokoyama, 1920: p. 174, pl. 18, fig. 20a–c; Taki and Oyama, 1954: pl. 19, fig. 20; Oyama, 1973: p. 76, pl. 21, fig. 15a–c (as paratype: error). Present status: Figured non-type specimen, missing. UMUT CM24546: Yokoyama, 1920: p. 174, pl. 18, fig. 21a–c; Taki and Oyama, 1954: pl. 19, fig. 21; Oyama, 1973: p. 76, pl. 21, fig. 19a–c (as

paratype: error). Present status: Figured non-type specimen, missing. UMUT CM20676: Yokoyama, 1920. p. 174, not figured. Present status: Unfigured non-type specimen, present in UMUT. UMUT CM20677: Yokoyama, 1920. p. 174, not figured. Present status: Unfigured non-type specimen, missing.

Limopsis truncata Yokoyama, 1910: UMUT CM26404: Yokoyama, 1910: p. 4, pl. 9, fig. 13 (as syntype). Present status: Lectotype designated in this study, present in UMUT (Figure 6C, D). UMUT CM26405: Yokoyama, 1910: p. 4, pl. 9, fig. 14. Present status: Paralectotype designated in this study, present in UMUT.

Five New Cenozoic Epitoniids from Southern Peru and the Neogene History of *Scalina* Conrad, 1865 (Gastropoda: Epitoniidae) in the Americas

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Abstract. Five new fossil species of the epitoniid genus, *Scalina* Conrad, 1865, are reported from the Pisco Basin of southern Peru: *S. foosei*, sp. nov. (late Eocene), *S. brophyi*, sp. nov. (early Miocene), *S. belti*, sp. nov. (early Miocene), *S. isaacsoni*, sp. nov. (middle Miocene), and *S. cheneyi*, sp. nov. (late Miocene to early Pliocene). *Scalina ferminiana* (Dall, 1908) is formally reported for the first time from upper Pliocene beds of northern Peru. During the Paleogene, American species of *Scalina* ranged from the northeastern Pacific Ocean to southern Peru and throughout the Gulf of Mexico. Neogene American taxa from warm subtropical and tropical waters with uncertain Paleogene ancestry are assigned to one of three groups arising from within a ‘*brophyi*’ clade: an ‘*isaacsoni*’ clade of sharply reticulate taxa extending from the middle Miocene to Recent that presently inhabit the eastern Pacific Ocean and both western and eastern Atlantic Ocean, a ‘*pseudoleroyi*’ clade of broad-spined species with anteriorly ramped spiral cords that arose during the late Miocene and persists today in the eastern Pacific and western Atlantic Oceans, and a ‘*brunneopicta*’ clade of narrow-spined populations with numerous spiral cords that also arose during the late Miocene and exists today only in the eastern Pacific Ocean. The most significant American Tethyan radiation of *Scalina* took place well before the closure of the Isthmus of Panama.

INTRODUCTION

Epitoniid gastropods of the genus *Scalina* Conrad, 1865, can be distinguished from cancellate species of *Amatea* H. Adams & A. Adams, 1853, by their contrasting basal and lateral spiral sculpture. Five Recent species of *Scalina* have been described from the eastern Pacific Ocean (Weil et al., 1999). *Scalina ferminiana* (Dall, 1908) ranges from Mexico to northern Peru (Dall, 1908a; Alamo & Valdivieso, 1997). The other four species are found only on the Mexican or Central American coast [*S. brunneopicta* (Dall, 1908), see Dall (1908a), *S. tehuacanum* (DuShane & McLean, 1968)], only in the Galapagos [*S. pompholyx* (Dall, 1890)], or from Mexico to the Galapagos [*S. deroyae* (DuShane, 1970)]. Two species of *Scalina* are recognized in the western Atlantic Ocean: *S. mitchelli* (Dall, 1896) and *S. retifera* (Dall, 1889). The latter species also occurs in the eastern Atlantic Ocean (Ardovini & Cossignani, 2004).

Several Neogene species of *Scalina* have been described from the eastern Pacific and western Atlantic Oceans, including taxa from Maryland (Martin, 1904), Jamaica (Guppy, 1874; Woodring, 1928), Venezuela (Jung, 1965), Panama (Olsson, 1942; Woodring, 1959), Mexico

(Böse, in Böse & Toula, 1910; DuShane, 1977), California (Keen, 1943; Addicott, 1970), Ecuador (Pilsbry & Olsson, 1941; DuShane, 1988), and northern Peru (DeVries, 1986). No fossils of *Scalina* had been reported from southern Peru, nor have any yet been described from Chile (e.g., Philippi, 1887; Tavera, 1979; Nielsen et al., 2004). Paleogene species of *Scalina* are widespread in North America, with species ranging from Alaska, possibly (Durham, 1937), and Washington State (Durham, 1937; Weaver, 1942) to the southeastern United States (MacNeil & Dockery, 1984); none had been reported from western South America.

This paper documents late Pliocene occurrences of *Scalina ferminiana* in northern Peru, the first Miocene and Pliocene examples of *Scalina* from southern Peru, the first Eocene species of *Scalina* from western South America, and addresses the late Cenozoic evolutionary history of *Scalina* in the Americas.

GEOLOGY

The stratigraphy of the Cenozoic Pisco Basin in southern Peru (Figure 1) has been described by Muizon & DeVries (1985), Dunbar et al. (1990), DeVries & Schrader (1997), DeVries (1998, 2004), and DeVries et al. (2006). Within this forearc basin, the middle to upper Eocene Paracas Formation overlies crystalline bedrock. Unconformably overlying the Paracas de-

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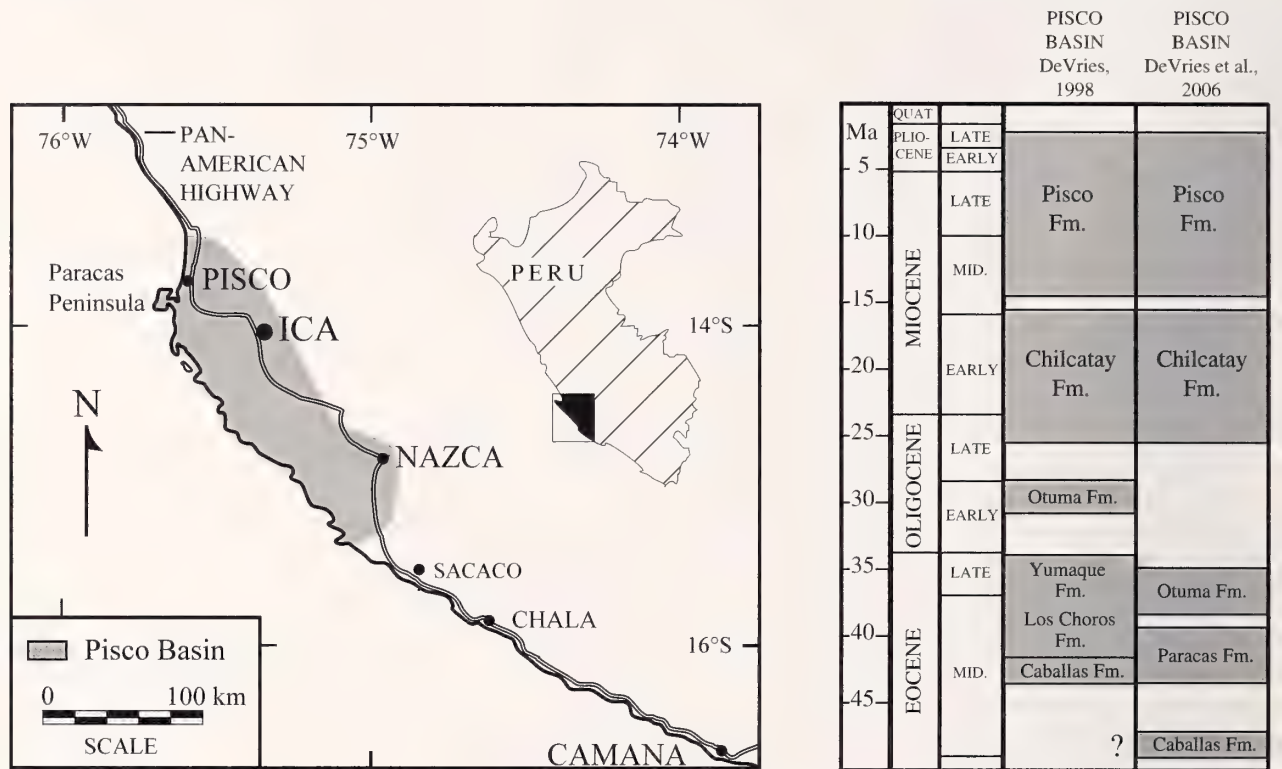


Figure 1. Locality and Cenozoic stratigraphy of the Pisco Basin in southern Peru. Specimens of *Scalina* occur in the Otuma, Chilcatay, and Pisco Formations.

positional sequence is the uppermost Eocene Otuma Formation, which in turn is overlain by the uppermost Oligocene to middle Miocene Chilcatay Formation and middle Miocene to Pliocene Pisco Formation. Each Cenozoic formation is characterized by a transgressive sandstone member representing nearshore paleoenvironments and a finer-grained, tuffaceous, and diatomaceous silty sandstone member representing outer shelf paleoenvironments. Fossils of *Scalina* are usually found in the nearshore sandstones.

METHODS AND MATERIALS

All Peruvian fossils in this study were found by the author. Geochronologic ages are reported by Muizon & DeVries (1985), Dunbar et al. (1990), DeVries (1998), and DeVries et al. (2006).

Spiral sculpture on specimens of *Scalina* is described according to a protocol previously employed with *Turritella* (Allmon, 1996; DeVries, 2007). Primary spiral cords are designated from anterior to posterior as 'E,' 'D,' 'C,' 'B,' and 'A' (Figure 2). Single or multiple secondary cords near the posterior suture are designated 'r,' 'rr,' 'rrr,' etc., and those near the anterior suture, 'w,' 'ww,' 'www,' etc. Secondary cords intercalated between primary spiral cords are designated in the following manner: EvDuCtBsA. Weak

primary spiral cords are listed in lower case; strong secondary cords are listed in upper case.

The principal shell characters used for distinguishing species of American *Scalina* include spire angle, whorl convexity, depth of suture, number of axial costae, lamellar extensions on costae, arrangement of primary spiral cords, presence of anterior ramping on primary spiral cords, complexity of secondary spiral cords, development of basal spiral cords, convexity of the basal region, and presence of a primary spiral cord bounding the basal region. The basal region may be entirely raised (a basal disk) or follow the contour of the anterior part of the body whorl.

Abbreviations for depositories for fossil specimens and localities are as follows: ANSP – Academy of Natural Sciences of Philadelphia, Pennsylvania, USA; FMNH – Florida Museum of Natural History, Gainesville, Florida, USA; LACM – Natural History Museum of Los Angeles County, California, USA; LACMIP – Natural History Museum of Los Angeles County, Invertebrate Paleontology; MUSM INV – Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; OSU – Orton Museum, Ohio State University, Columbus, USA; PRI – Paleontological Research Institution, Ithaca, New

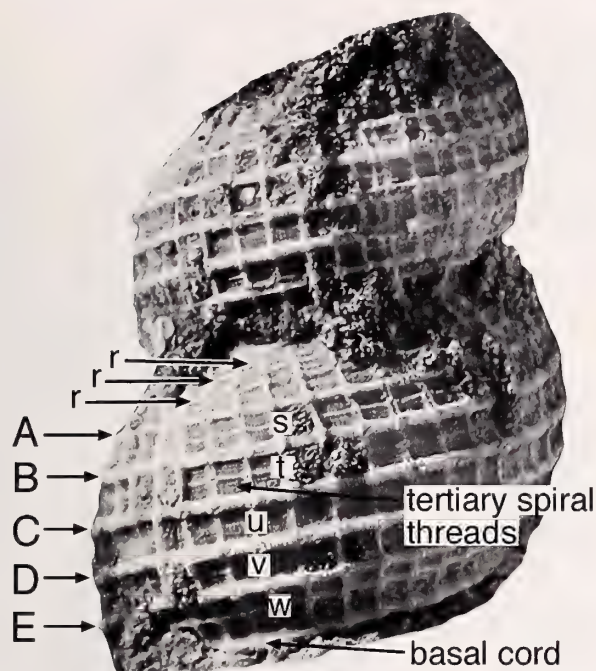


Figure 2. Arrangement and naming of spiral sculpture on *Scalina*. Primary spiral cords are labeled 'A,' 'B,' 'C,' 'D,' and 'E' between the posterior suture and anterior basal cord; intervening secondary spiral cords are labeled 'r,' 's,' 't,' 'u,' 'v,' and 'w' in the same direction.

York, USA; UCMP – University of California, Museum of Paleontology, Berkeley, USA; USGS – United States Geological Survey [Washington, D.C. register or Menlo Park, California, register (M series)]; many of the USGS specimens cited herein are now at UCMP; UWBM – Burke Museum of Natural History and Culture, University of Washington, Seattle, USA.

Museum numbers are followed by locality-sample numbers that are listed in the Appendix. Measurements of length (L) and width (W) are in millimeters. Numbers enclosed by parentheses indicate sizes for broken or deformed specimens. Specimens were coated with ammonium chloride prior to photography.

SYSTEMATIC PALEONTOLOGY

Family Epitoniidae S. S. Berry, 1910

Genus *Scalina* Conrad, 1865

Type species: (by subsequent designation, Palmer, 1937) *Scalina staminea* Conrad, 1865.

Ferminoscala Dall, 1908, p. 315.

Discussion: Some authors have assigned cancellate epitoniids with differentiated basal sculpture to *Amaea* (*Scalina*) [*Amaea* H. Adams & A. Adams, 1853; type

species by subsequent designation (Melville, 1897): *Scalaria magnifica* Sowerby II, 1844]]. Data in this paper show that the diagnostic characters of *Scalina* have persisted within a monophyletic clade in the Americas since the early Miocene. It seems probable that the same characters unite a larger and more widely distributed group of Neogene *Scalina* species that is rooted in the Eocene, from which epoch numerous species of *Scalina* have also been identified (e.g., for the Americas, Durham, 1937; Weaver, 1942; MacNeil & Dockery, 1984). Because of the persistence of diagnostic characters, the longevity of the taxon, and its species richness, *Scalina* is herein assigned full generic rank, as has been done by others (e.g., Woodring, 1959; Olsson, 1964; Addicott, 1970; MacNeil & Dockery, 1984).

Scalina ferminiana (Dall, 1908)

Figures 3, 4, 6, 8–11

Epitonium (*Ferminoscala*) *ferminianum* Dall, 1908, p. 316, pl. 8, fig. 8.

Epitonium (*Ferminoscala*) *ferminianum* Dall. Olsson, 1942, p. 76, pl. 9, fig. 6.

Scalina ferminiana (Dall). Olsson, 1964, p. 200, pl. 33, figs. 2, 2a.

Amaea (*Scalina*) *ferminiana* (Dall, 1908). DuShane, 1974, p. 53, figs. 65, 68.

Amaea (*Scalina*) *ferminiana* (Dall, 1908). Peña, 1976, p. 2, fig. 2.

Amaea (*Scalina*) *ferminiana* (Dall, 1908). DeVries, 1986, p. 535, pl. 28, fig. 16.

Amaea (*Scalina*) *ferminiana* (Dall, 1908). DuShane, 1988, p. 53, figs. 2, 3.

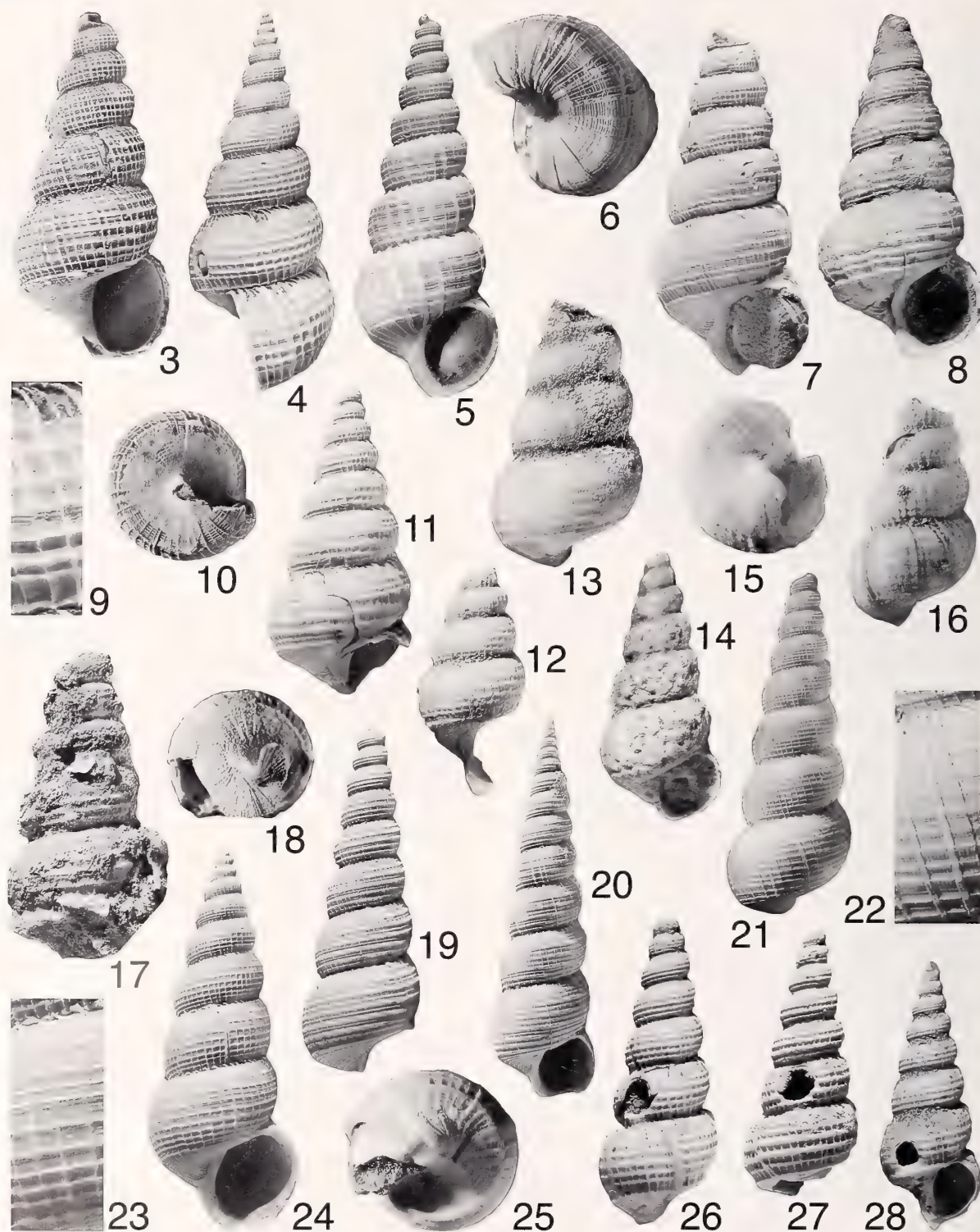
Amaea (*Scalina*) *ferminiana* (Dall). Alamo & Valdivieso, 1997, p. 26, fig. 68.

Scala (*Acrilla*) *weigandi* Böse, 1910, p. 259, pl. 12, fig. 8. Not *Scalina weigandi* (Böse). Woodring, 1959, p. 187, pl. 29, figs. 7, 8 (= *Scalina* aff. *S. isaacsoni*, sp. nov.).

Epitonium (*Ferminoscala*) *manabianum* Pilsbry & Olsson, 1941, p. 37, pl. 2, fig. 3.

Diagnosis: Shell length to 80 mm. Spire angle 24 to 26 degrees. Weakly and irregularly reticulate. Primary spiral cords ramped anteriorly. Basal disk not bounded by primary spiral cord.

Description: Shell length to 80 mm. Spire angle 24 to 26 degrees. Whorls moderately convex, shoulder evenly rounded; sutures moderately impressed. Protoconch not seen. Teleoconch of 13 whorls. Sculpture weakly reticulate, spiral elements stronger. Axial sculpture of 50 to 80 subequally spaced thin costae; a few irregularly spaced costae thickened. Costae stand well below spiral cords; slightly lamellate at posterior suture. Adult spiral formulae EDCBAr, wwEDCBArRrr, wEDC-



Figures 3, 4, 6, 8-11. *Scalina ferminiana* (Dall, 1908). Figure 3. LACMIP 7630. Pliocene, Ecuador. Apertural view. Length is 16.1 mm. Figure 4. PRI 4065. Panama, Pliocene-Pleistocene. Lateral view. Length is 41.1 mm. Figure 6. OSU 37549, DV 267-3. Northern Peru, Pliocene. Oblique view of base. Width is 15.4 mm. Figure 8. OSU 37548, DV 267-3. Apertural view. Length is 53.7 mm. Figure 9. PRI 4065. Close-up of sculpture showing anterior ramps and overlay of tertiary spiral threads on primary spiral

BARrrr, or wEDCBAr. Primary spiral cords evenly spaced, except 'D' closer to 'E.' Spiral cords ramped anteriorly and steeply rounded posteriorly. Interspaces with strong tertiary spiral threads, often superimposed upon primary spiral cords; interspaces also with tertiary axial threads. Basal disk present, weakly to moderately inclined, planar, with 30 closely spaced secondary spiral threads, extensions of weak costae, and tertiary spiral and axial threads; not bounded by primary spiral cord. Aperture ovate, moderately spatulate at base of columella; outer lip variably thickened. Umbilicus absent.

Type Locality: U.S.S. 'Albatross' station 2834, off Baja California, 87 m, mud bottom. Recent.

Discussion: Pliocene specimens of the Ecuadorian *Epitonium* (*Ferminoscala*) *manabianum* are placed in synonymy with *Scalina ferminiana*, as is the middle Pliocene (Akers, 1981) holotype of *S. weigandi* from the Caribbean side of the Isthmus of Tehuantepec, Mexico, because of their wide spire angles, anteriorly ramped spiral cords, and tertiary spiral threads incised prominently over the primary spiral cords. Specimens of *S. pseudoleroyi* (Maury, 1925) from the upper Pliocene Bowden Formation of Jamaica (Woodring, 1928; Pickerill et al., 1998) and upper Miocene Gatun beds of Panama (Woodring, 1959; Coates et al., 1992) typically have narrower spire angles than specimens of *S. ferminiana* and have a more complex differentiation of primary and secondary spiral cords. Specimens of the Recent Atlantic *S. mitchelli* are similar in size and shape to those of *S. ferminiana*, but have stronger and fewer axial costae and a spiral band of brown that is

not present on equally well preserved Recent specimens of *A. ferminiana*.

Individuals of *Scalina ferminiana* presently live at shelf depths from Baja California to Paita, Peru (DuShane, 1974; Peña, 1976; Alamo & Valdivieso, 1997). Examples in LACM collections obtained live and dead between 15°58'N and 4°57'S were nearly always found on soft sediment at water depths greater than 36 m. Pliocene individuals from the Esmeraldas beds of Ecuador, Tehuantepec outcrops of southern Mexico, and Charco Azul outcrops of Panama occupied deep-water environments (Olsson, 1942, 1964; DuShane, 1988). Specimens from the upper Pliocene or Pleistocene Canoa Formation of Ecuador came from mid-shelf depths (Pilsbry & Olsson, 1941; Bianucci et al., 1997; Collins, 2006). Upper Pliocene specimens from the Taime Formation of northern Peru, in contrast, were found in fine-grained sandstones once deposited in a lagoon (DeVries, 1986, 1988).

Material: ANSP 13641, holotype, *Epitonium* (*Ferminoscala*) *manabianum* Pilsbry & Olsson, 1941, Ecuador, Pliocene, L (37.7), W (17.9); LACMIP 7631, LACMIP locality 11794, Ecuador, Pliocene, L (24.9), W 10.8; LACMIP 7630, hypotype, LACMIP locality 11794, L 16.1, W 7.3; OSU 37548, DV 267-3, northern Peru, late Pliocene to early Pleistocene, L 53.7, W 25.7; OSU 37549, DV 267-3, L 33.4, W 15.4; OSU 37550, DV 236-3, northern Peru, late Pliocene to early Pleistocene, L (41), W (22); PRI 4065, Panama, Pliocene to Pleistocene, L 41.1, W (15.4).

Occurrence: Late Pliocene: Southern Mexico (Caribbean); Panama to Ecuador and northern Peru. Recent: Gulf of California to northern Peru.

cords. Figure 10. LACMIP 7630. Basal view. Width is 7.3 mm. Figure 11. ANSP 13641. Holotype of *Epitonium* (*Ferminoscala*) *manabianum* Pilsbry & Olsson, 1941. Ecuador, Pliocene. Apertural view. Outer lip is missing. Length is 37.7 mm.

Figure 5. *Scalina mitchelli* (Dall, 1896). FMNH 00128594, Texas, Recent. Apertural view. Medial brown band visible beneath light coating of ammonium chloride. Length is 47.1 mm.

Figure 7. *Scalina pseudoleroyi* (Maury, 1925). USNM 562623, USGS locality 8410. Panama Canal Zone, Pliocene. Apertural view. Length is 35.5 mm.

Figures 12–18. *Scalina cheneyi*, sp. nov. Figure 12. UWM 98094, DV 571-6, syntype. Southern Peru, late Miocene. Apertural view, outer lip missing. Length is 12.2 mm. Figure 13. MUSM INV 144, DV 571-6, syntype. Abapertural view. Length is 16.2 mm.

Figure 14. UWM 98095, DV 599-2. Southern Peru, late Miocene. Apertural view, replaced with gypsum and severely pitted. Length is 24.0 mm. Figure 15. MUSM INV 145, DV 571-6. Basal view. Width is 5.9 mm. Figure 16. UWM 98092, DV 571-6. Abapertural view. Length is 12.8 mm. Figure 17. MUSM INV 146, DV 523-2. Southern Peru, early Pliocene. Lateral view. Length is 32.2 mm. Figure 18. UWM 98094. Basal view. Width is 5.6 mm.

Figures 19–22. *Scalina brunneopicta* (Dall, 1908). Figure 19. ANSP 13640, holotype of *Epitonium eleutherium* Pilsbry & Olsson, 1941. Ecuador, Pliocene. Apertural view, outer lip and columella missing. Length is 21.1 mm. Figure 20. LACM 127965. Mexico, Recent. Apertural view. Length is 36.8 mm. Figure 21. LACM 38-8. Mexico, Recent. Abapertural view. Length is 32.1 mm. Figure 22. LACM 38-8. Close-up of sculpture.

Figures 23, 24. *Scalina tehuanaorum* (DuShane & McLean, 1968). Figure 23. LACM 1162, holotype. Mexico, Recent. Close-up of sculpture. Figure 24. LACM 1162. Apertural view. Length is 39.5 mm.

Figures 25–28. *Scalina whitei* (Keen, 1943). Figure 25. USGS M2480, specimen 1. California, middle Miocene. Basal view. Width is 8.0 mm. Figure 26. USGS M2480, specimen 1. Abapertural view. Length is 21.3 mm. Figure 27. UCMP B1638, specimen 15430. California, middle Miocene. Abapertural view. Length is 12.9 mm. Figure 28. USGS M1613, specimen 1. California, middle Miocene. Apertural view. Length is 16.7 mm.

Scalina mitchelli (Dall, 1896)

Figure 5

Scala mitchelli Dall, 1896, p. 112.

Amaea (*Amaea*) *mitchelli* (Dall). Clench & Turner, 1950, p. 243, pl. 106, figs. 5–7.

Amaea mitchelli (Dall). Princz, 1982, p. 174–175.

Diagnosis: Shell length to 65 mm. Spire angle 20 to 26 degrees. Axial costae strong, irregularly thickened; fewer than 45 on body whorl. Primary spiral cords ramped anteriorly; intercalated secondary spiral cords often present.

Description: Shell length to 65 mm. Spire angle 20 to 26 degrees. Whorls moderately convex, shoulders evenly rounded, sutures moderately impressed. Protoconch unknown. Teleoconch of 14 to 15 whorls; early whorls posteriorly angulate at periphery. Sculpture reticulate, axial elements as strong or stronger than spiral elements. Axial sculpture of 20 to 45 costae, several irregularly thickened, often slightly lamellose at posterior suture. Adult spiral formula wEDuCBarr or with additional intercalated strong secondary spiral cords and strong tertiary threads; spacing of primary spiral cords subequal. Primary spiral cords ramped usually anteriorly. Basal disk present, moderately inclined, planar to slightly convex, with about 20 to 40 closely spaced mixed secondary spiral cords and tertiary spiral threads, and strong extensions of axial costae; bounded by 1 to 3 flattened primary spiral cords or unbounded. Aperture ovate, spatulate at base of columella. Outer lip sometimes thickened. Umbilicus absent. Whorls with medial brown band, one-third of whorl's axial length, and brown basal disk.

Type Locality: Beach drift, Matagorda Island, Texas. Recent.

Discussion: *Scalina mitchelli* is sometimes placed in *Amaea* (*Amaea*) (e.g., Clench & Turner, 1950), but its differentiated basal region, clearly noted by Dall (1896), places it with *Scalina* (DuShane, 1974; MacNeil & Dockery, 1984). Specimens of *S. mitchelli* have fewer and coarser axial costae than either *S. ferminiana* or a similar fossil species, *S. pseudoleroyi*, but as many intercalated secondary spiral cords as specimens of the latter species.

Material: FMNH 145466, Gulf of Mexico, Mexico, Recent, L (49.6), W 20.5; W 17.4; FMNH 152778, Gulf of Mexico, Mexico, Recent, L 57.0, W 18.5; FMNH 00128594, Texas, Recent, L 47.1.

Occurrence: Recent: Gulf of Mexico, Caribbean, Venezuela (Princz, 1982).

Scalina pseudoleroyi (Maury, 1925)

Figure 7

Epitonium (*Acrilla*) *pseudoleroyi* Maury, 1925, p. 243.

Ferminoscala pseudoleroyi (Maury). Woodring, 1928, p. 402, pl. 32, figs. 3, 4.

Scalina pseudoleroyi (Maury). Woodring, 1959, p. 187, pl. 38, figs. 6, 21.

Not *Scalina pseudoleroyi* (Maury). Jung, 1965, p. 493, pl. 65, fig. 6 (= *Scalina belti*, sp. nov.).

Scalaria leroyi Guppy. Guppy 1874, p. 406, pl. 16, fig. 10. Not pl. 18, fig. 2.

Not *Scalaria leroyi* Guppy, 1867, p. 168.

Diagnosis: Shell length about 40 mm. Spire angle about 20 degrees. Primary spiral cords ramped anteriorly; tertiary spiral threads encroach upon primary spiral cords; some intercalated secondary spiral cords. Basal disk not bounded by spiral cord.

Description: Shell length about 40 mm. Spire angle about 20 degrees. Whorls moderately convex, shoulder evenly rounded, sutures moderately impressed. Protoconch unknown; broken teleoconch of at least six whorls. Sculpture moderately reticulate. Axial sculpture of 40 to 70 costae standing slightly above primary spiral cords; some cords lamellate, especially at posterior suture; others thickened at irregular intervals. Spiral formula wwWEDCBsArrrr; primary spiral cords evenly spaced; interspace between 'E' and anterior suture broad. Primary spiral cords thin, ramped anteriorly. Strong tertiary spiral threads intercalated with and encroaching upon primary spiral cords. Basal disk moderately inclined, planar or slightly convex, with about 25 to 30 closely spaced secondary spiral cords; also with extensions of axial costae; not bounded by primary spiral cord. Aperture ovate, slightly spatulate at base of columella. Umbilicus absent.

Type Locality: Jamaica. Pliocene.

Discussion: As noted by Woodring (1959), the Gatun specimens of *Scalina pseudoleroyi* are more similar to the eastern Pacific *S. ferminiana* than either Recent Atlantic species (*S. mitchelli*, *S. retifera*) assigned to *Scalina*, differing from *S. ferminiana* by having a narrower spire angle, more prominent axial costae, and weaker primary spiral cords. The spiral sculptural pattern is very much like that of *S. tehuaranum*, but the latter species has many fewer basal secondary spiral cords and a spire that uniquely among *Scalina* species changes its angle along its length.

Material: USNM 562623, USGS locality 8410, Panama, Pliocene, L (35.5), W 15.4; USNM 115437, holotype, Jamaica, Pliocene, L (25.3), W 13.4.

Occurrence: Pliocene: Caribbean.

Scalina cheneyi, sp. nov.

Figures 12–18

Diagnosis: Spire angle about 21 degrees. Primary spiral cords low, broad, wider than interspaces. Basal disk not bounded by spiral cord.

Description: Shell length to 50 mm. Spire angle 21 degrees. Whorls moderately and evenly convex, sutures moderately impressed. Protoconch unknown. Spire incomplete; teleoconch with at least six whorls. Sculpture subdued; spiral elements stronger. Axial sculpture of 44 to 55 costae; costae rise slightly above spiral cords, with lamellar extensions sometimes present at one or both sutures. Spiral formula wEDuCBarr, also wwEDCBarr. Primary spiral cords low, broad, sometimes anteriorly ramped, wider than interspaces; unevenly spaced, 'D' closer to 'E.' Basal disk present, with about 12 secondary spiral threads; not bounded by primary spiral cord. Aperture oval to almost circular; base of columella / inner lip slightly spatulate. Outer lip thin. Umbilicus absent.

Type Locality: DV 571-6, Alto Grande, at the northern edge of the Sacaco Basin, southern Peru, in a sublittoral shell lag or intertidal beach deposit near the base of the Pisco Formation (Figure 29). Lower upper Miocene.

Discussion: Specimens of late Miocene and early Pliocene *Scalina cheneyi* differ from those of the younger *S. ferminiana* by having a narrower spire, deeper sutures, and broad primary spiral cords with less well-developed tertiary spiral threads. They differ from specimens of the middle Miocene Peruvian *S. isaacsoni* and all older Neogene Peruvian species by lacking sharply rounded, widely spaced spiral cords and by having a larger spire angle. The broad spiral cords of *S. cheneyi* resemble those on specimens of Recent *S. brunneopicta*, although specimens of the latter have many more primary spiral cords and a much narrower spire angle.

Etymology: Named for Jack Cheney, the author's professor of igneous and metamorphic petrology at Amherst College in 1976.

Material: MUSM INV 144, DV 571-6, syntype, Peru, late Miocene, L (16.2), W 9.1; MUSM INV 145, DV 571-6, syntype, L (9.6), W 5.9; MUSM INV 146, DV 523-2, Peru, early Pliocene, L (32.2), W 14.4; UWBM 98092, DV 571-6, syntype, L (12.8), W (6.7); UWBM 98093, DV 571-6, syntype, L (19.1), W (8.3); UWBM 98094, DV 571-6, syntype, L (12.2), W (5.6); UWBM 98095, DV 599-2, Peru, late Miocene, L (24.0), W 10.7; UWBM 98096, DV 599-2, L (14.6), W 8.5; UWBM 98097, DV 599-2, lot of 11; UWBM 98098, DV 523-2, L (32.9), W 15.2; UWBM 98099, DV 523-4, Peru, early

Pliocene, L (27.0), W (11.3); UWBM 98106, DV 1348-1, southern Peru, late Miocene, L (18.2), W 8.9.

Occurrence: Early late Miocene to early Pliocene: southern Peru.

Scalina brunneopicta (Dall, 1908)

Figures 19–22

Epitonium (Ferminoscala) brunneopictum Dall, 1908, p. 316, pl. 8, fig. 10.

Amaea (Scalina) brunneopicta (Dall, 1908). DuShane, 1974, p. 53, figs. 63, 64, 68.

Amaea (Scalina) brunneopicta (Dall, 1908). DuShane, 1979, p. 97, figs. 3, 4.

Scalina cf. *S. brunneopicta* (Dall). Woodring, 1959, p. 188, pl. 38, figs. 7, 14.

Epitonium (Ferminoscala) eleutherium Pilsbry & Olsson, 1941, p. 38, pl. 2, fig. 7.

(?) *Scalina mitchelli* (Dall). Perrilliat, 1972, p. 53, pl. 25, figs. 8–13.

Diagnosis: Spire angle about 14 degrees. Costae irregularly thickened, not lamellar. Primary and secondary spiral cords equally strong, broad or asymmetrically triangular.

Description: Shell length to 44 mm. Spire angle about 14 degrees. Whorls weakly convex, shoulder steeply inclined, sutures weakly to moderately impressed. Protoconch unknown. Teleoconch of 13 to 14 whorls. Sculpture very weakly reticulate. Axial sculpture of 40 to 45 thin, unevenly spaced costae barely standing as high as spiral cords except several irregularly spaced thickened costae. Costae slightly extended at posterior suture. Earliest teleoconch whorl posteriorly angulate with spiral formula bCd; subsequent whorls with spiral formulae edCb, EDCBa, wEDCBa, wEDuCBa, WEvDuCtBsAr, and on body whorl, WEvDUCTBsArr; also WEVDUCTBArrrr. Primary spiral cords evenly spaced. Spiral cords broad and flattened or anteriorly ramped; as wide or wider than interspaces. Interspaces with tertiary spiral threads and very faint axial threads. Basal disk nearly fully formed, moderately inclined, planar, with 12 to 16 closely spaced secondary spiral cords and intervening tertiary spiral threads, extensions of costae, and axial threads; bounded by weak spiral cord. Aperture ovate, weakly to moderately spatulate at base of columella. Outer lip thin. Umbilicus absent.

Type Locality: U.S.S. 'Albatross' station 2835, 10 m water depth, mud bottom, off Baja California. Recent.

Material: LACM 127965, Sonora, Mexico, Recent, L 36.8, W 10.0; LACM 38-8, Guerrero, Mexico, Recent, specimen 1, L 32.1, W 11.2; LACM 38-8, specimen 2, L

29.0, W 9.1; ANSP 13640, holotype of *Epitonium eleutherium* Pilsbry & Olsson, 1941, Ecuador, Pliocene, L 21.1, W 6.9.

Discussion: The Pliocene Ecuadorian *Epitonium eleutherium* does not differ in any significant respect from specimens of Recent *Scalina brunneopicta* in LACM collections and so is considered a junior synonym of the latter species. The small specimens of late Miocene *Scalina* cf. *S. brunneopicta* Woodring, 1959, from the upper Gatun Formation of Panama have broad primary spiral cords but lack the intercalation of strong secondary with primary spiral cords seen on adult specimens of *S. brunneopicta*; they may be juveniles. Specimens from the middle Pliocene Agueguexquite Formation of Mexico (Perrilliat, 1972; Akers, 1981) are more elongate than those of *S. mitchelli*, to which they were assigned; they are more similar to specimens of *S. brunneopicta*.

Occurrence: Late Miocene: Panama. Pliocene: Southern California to Ecuador. Recent: Gulf of California and Baja California to Ecuador.

Scalina tehuanaarum (DuShane & McLean, 1968)

Figures 23, 24

Amaea (Scalina) tehuanaarum DuShane & McLean, 1968, p. 4, figs. 4, 5.

Amaea (Scalina) tehuanaarum DuShane & McLean, 1968. DuShane, 1974, p. 56, fig. 68.

Amaea (Scalina) tehuanaarum DuShane & McLean, Alamo & Valdivieso, 1997, p. 26.

Amaea (Scalina) tehuanaarum DuShane & McLean, 1968. Weil et al., 1999, fig. 445.

Diagnosis: Spire angle varies along length of shell. Body whorl with eight to nine strong spiral cords, spaced at diminishing intervals anteriorly. Outer lip thickened.

Description: Shell length to 50 mm. Spire angle varies from 25 degrees posteriorly to 20 degrees anteriorly. Whorls weakly to moderately convex, shoulder short, weakly tabulate, sutures weakly impressed. Protoconch unknown. Teleoconch of at least nine whorls. Sculpture moderately reticulate. Axial sculpture of 47 equally spaced thin costae standing slightly higher than spiral cords; several costae thickened at irregular intervals. Costae often extended adapically at posterior suture. Earliest visible whorl angulate with spiral formula edcB, followed by edcBa, wEDCBarr, wWEDCBARR, and on body whorl, wWEDuCbArrRrrr. Primary spiral cords rounded, ramped anteriorly, evenly spaced on periphery, increasingly closely spaced anteriorly. Interspaces with strong tertiary spiral threads and obsolete axial threads. Basal disk partly formed; basal region steeply

inclined, convex, with 12 evenly spaced secondary spiral cords and extensions of costae; interspaces with axial threads and obsolete spiral threads; bounded by weak spiral cord. Aperture oval, moderately spatulate at base of columella. Outer lip thickened. Umbilicus absent.

Type Locality: Gulf of Tehuantepec, Mexico, 59 to 68 m water depth, mud bottom. Recent.

Discussion: The shape of the primary spiral cords, the coarseness of the secondary spiral cords on the basal region, and adapical extension of costae at the shoulder on the holotype of *Scalina tehuanaarum* is like that on specimens of *S. brunneopicta*. The large spire angle is like that of *S. ferminiana*, although the spire of *S. tehuanaarum* is uniquely bowed.

Material: LACM 1162, holotype, Mexico, Recent, L 39.5, W 14.9.

Occurrence: Recent: Gulf of California to northern Peru (DuShane, 1974; Alamo & Valdivieso, 1997; Weil et al., 1999).

Scalina whitei (Keen, 1943)

Figures 25–28

Ferminoscala whitei Keen, 1943, p. 46, pl. 4, figs. 32, 33. *Scalina whitei* (Keen). Addicott, 1970, p. 56, pl. 3, figs. 20, 25–28.

Ferminoscala durhami Keen, 1943, p. 46, pl. 4, fig. 31. *Scalina durhami* (Keen). Addicott, 1970, p. 56, pl. 3, figs. 21, 24.

Not *Acrilla (Ferminoscala) durhami* Zinsmeister, 1983, p. 1291, figs. 2N, 2O.

(?) *Scalina* sp. Perrilliat, 1992, p. 23, pl. 7, fig. 1.

Diagnosis: Shell length to 24 mm. Shoulder steeply inclined. Primary spiral cords broad, sometimes thickened; often intercalated with secondary primary cords. Basal region with eight secondary spiral cords.

Description: Shell length to 24 mm. Spire angle 19 to 21 degrees. Whorls moderately convex; sutures moderately impressed; shoulder broad, steeply inclined. Protoconch unknown. Teleoconch of 13 whorls; sculpture strongly reticulate. Axial sculpture of 42 to 45 thin costae, uniformly spaced and level with spiral cords, occasionally thick and standing above spiral cords. Costae often with small, adaxially hooked, recurved or upright extensions on shoulder. Spiral sculpture wEDCBarr, EDCBARR, or wEvDuCbArrrr (hypotype); 'r' and 'A' on shoulder. Primary spiral cords 'A,' 'B,' 'C,' 'D,' and 'E' thick, evenly convex or flattened, width variable; 'B,' 'C,' and 'D' strongest. Interspaces with minute reticulation of spiral and axial threads. Basal disk absent; basal region steeply in-

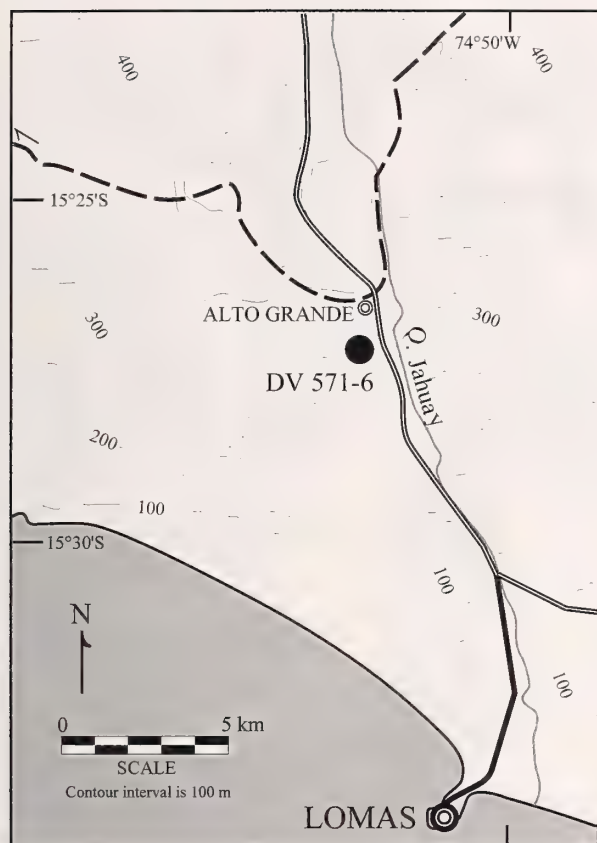


Figure 29. Type locality (DV 571-6) of *Scalina cheneyi*, sp. nov., along Panamerican Highway near Alto Grande, southern Peru.

clined, planar, with eight secondary spiral cords, extensions of axial costae, and minute tertiary spiral and axial threads; bounded by strong primary spiral cord. Aperture ovate, slightly spatulate anterior to columella. Outer lip thin. Umbilicus absent.

Type Locality: LSJU locality 2121, six miles northeast of Edison, California. Round Mountain Silt, middle Miocene.

Discussion: Specimens of *Scalina whitei* are smaller than those of *S. isaacsoni*, slightly broader, with whorls that are more convex and spiral cords that are usually more closely spaced. The spiral sculptural formula of *S. whitei* is usually as simple as that of *S. isaacsoni*, although the hypotype shows a more complex spiral pattern reminiscent of early Miocene species of *Scalina* in southern Peru. *Scalina durhami* (Keen, 1943) appears to be a worn example of *S. whitei* from the same locality.

Specimens of *Scalina whitei* were collected by Keen (1943) and Addicott (1970) from the deep-water Olcese Sandstone and Round Mountain Silt of central California, units recently assigned ages of late early

Miocene and early middle Miocene, respectively (Sanchez, 2003). A poorly preserved specimen of *Scalina* from the middle Miocene Ferrotepec Formation on the central Pacific coast of Mexico (Perrilliat, 1992) may be referable to *S. whitei* or the middle Miocene Peruvian *S. isaacsoni*.

Material: (all material from California, middle Miocene) UCMP specimen 15430, UCMP B1638, L 12.9, W 5.7; UCMP B1601, lot of 1; USGS 6064, lot of 2; USGS M1608, lot of 1; USGS M1613, specimen 1, L 16.7, W 6.2; USGS M1613, lot of 15; USGS M2480, specimen 1, L 21.3, W 8.0; USGS M2480, lots of 3 and 4.

Occurrence: Early to middle Miocene: Southern California.

Scalina retifera (Dall, 1889)

Figures 30–34

Scala (Acrilla) retifera Dall, 1889, p. 312.

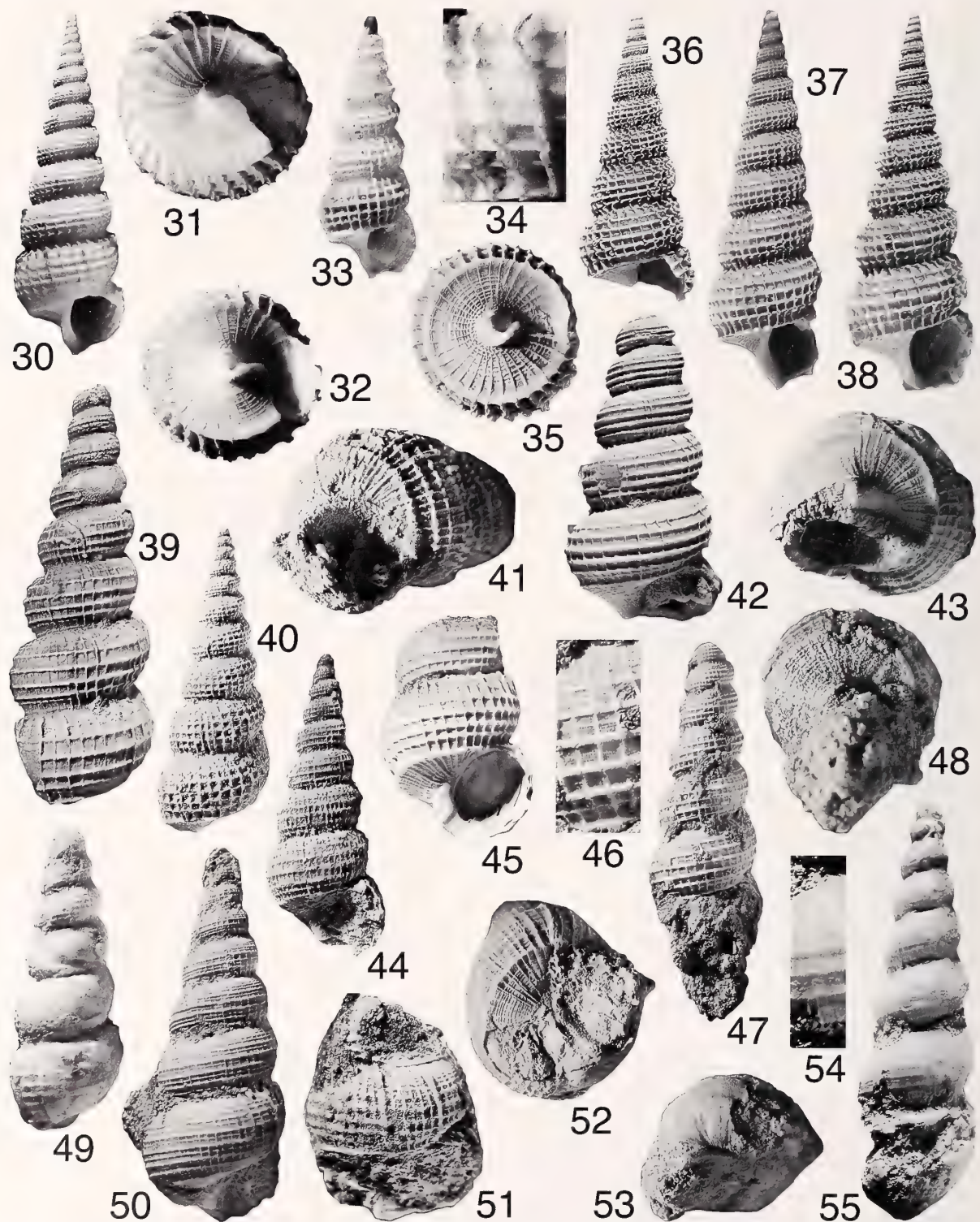
Amaea (Ferminoscala) retifera Dall. Clench & Turner, 1950, p. 243, pl. 96; pl. 106, figs. 1–4.

Amaea (Scalina) retifera (Dall, 1889). Ríos, 1985, pl. 53, fig. 745.

Amaea retifera. Ardovini & Cossignani, 2004, un-numbered figure, p. 137.

Diagnosis: Shoulder angulate, tabulate. Lamellar costae raised, extended adapically at shoulder. Secondary spiral cords between primary spiral cords generally absent.

Description: Shell length to 32 mm. Spire angle about 20 degrees. Whorls moderately convex, shoulder narrow, angulate, and slightly tabulate; sutures deeply impressed. Protoconch of three deviated translucent brown whorls with minute spiral and axial scratches. Teleoconch of 14 to 15 whorls; sculpture strongly reticulate. Axial sculpture of 26 to 30 evenly spaced, recurved, lamellar costae standing well above and scalloped across all spiral cords; costae weakly extended adaxially at shoulder. Earliest teleoconch whorl strongly angulate with spiral formula bCd. Subsequent whorls with spiral formulae edCb, eDCBa, eDCBa, EDCBar, wEDCBar, and wEDCBarr by sixth whorl. Body whorl with spiral formula wEDCBarr. Primary spiral cords evenly spaced; interspace between 'E' and anterior suture broad; 'B,' 'C,' and 'D' slightly stronger than 'A' and 'E.' Two secondary 'r' spiral cords very weak. Spiral cords raised, steeply rounded, half as wide as interspaces. Interspaces with spiral and axial tertiary threads. Basal disk absent; basal region weakly inclined, slightly concave, with about 30 tertiary spiral threads, extensions of axial costae, and minute tertiary axial threads; bounded by primary spiral cord.



Figures 30–34. *Scalina retifera* (Dall, 1889). Figure 30. LACM 164927, specimen 1. Florida, Recent. Apertural view. Length is 30.9 mm. Figure 31. LACM 164927, specimen 1. Basal view. Width is 9.7 mm. Figure 32. LACM 164927, specimen 2. Basal view. Width is 6.5 mm. Figure 33. DeVries collection, Panama (Caribbean), Recent. Apertural view showing deviated protoconch. Length is 6.7 mm. Figure 34. LACM 164927, specimen 1. Close-up of sculpture.

Aperture nearly circular, weakly spatulate anterior to columella. Outer lip thin. Umbilicus absent.

Type Locality: 27 to 40 km off the coast of North Carolina, U.S. Fish Commission Stations 2595 and 2596, in 89 to 115 m water depth; sand bottom. Recent.

Material: LACM 164927, Florida, Recent, specimen 1, L 30.9, W 9.7; LACM 164927, specimen 2, L 20.0, W 6.5; DeVries collection, Panama (Caribbean), Recent, L 6.7, W 2.2.

Discussion: The description of *Scalina retifera* by Clench and Turner (1950) is more detailed than that of Dall (1889) and consistent with the above description drawn from LACM material. The number of costae varies according to the size of the specimen but is less than the number seen on specimens of the Recent Pacific geminate species, *S. deroyae* or the middle Miocene Peruvian *S. isaacsoni*.

Occurrence: Recent: Gulf of Mexico, North Carolina to Brazil (Ríos, 1985) and West Africa (Weil et al., 1999; Ardovini & Cossignani, 2004).

Scalina deroyae (DuShane, 1970)

Figures 35–38

Amaea (*Scalina*) *deroyae* DuShane, 1970, p. 330, pl. 51, fig. 2.

Amaea (*Scalina*) *deroyae* DuShane, 1970. DuShane, 1974, p. 54, fig. 67.

Diagnosis: Shoulder rounded. Lamellar costae raised, radially extended posteriorly. Secondary cords weak or absent.

Description: Shell length to 22 mm. Spire angle 14 to 18 degrees. Whorls moderately convex, shoulder narrow,

steeply inclined; sutures weakly to moderately impressed. Protoconch unknown. Teleoconch of 14 whorls. Sculpture strongly reticulate. Axial sculpture of 31 to 34 upright to recurved lamellar costae standing above and scalloped across spiral cords; weakly extended radially or adapically at shoulder. Earliest teleoconch whorl evenly rounded with spiral formula bCd. Subsequent whorls with spiral formulae edCb, eDCBa, and wEDCBA. Body whorl with spiral formulae wEDCBA, wEDCBAr, or EDCBA; secondary cords 'r' and 'w' weakly developed or absent. Primary spiral cords evenly spaced, all nearly equal in size; interspace between 'E' and anterior suture not much broader than other primary spiral cord interspaces. Spiral cords steeply rounded, elevated, half as wide as interspaces. Interspaces with fine reticulation of tertiary spiral and axial threads. Basal disk absent; basal region weakly inclined, planar to deeply concave, with about nine secondary spiral cords closest to axis, intervening tertiary spiral threads, extensions of axial costae, and axial threads; bounded by strong primary spiral cord. Aperture ovate, nearly circular, weakly spatulate near columella. Outer lip thin. Umbilicus absent.

Type locality: Tagus Cove, Isla Isabela (Albemarle), Islas Galapagos, cruise of R/V Velero III, 55 m water depth, rock and coral bottom. Recent.

Material: LACM 1236 (AHF 147-34), holotype, Ecuador, Recent, L 22.6, W 6.6; LACM 128144, Mexico, Recent, L 19.8, W 6; LACM 55642, Mexico, Recent, specimen 1, L 14.0, W 4.5; LACM 55642, specimen 2, L (10.5), W 4.1; LACM 55642, specimen 3, L 22.4, W 7.1.

Discussion: Specimens of *Scalina deroyae* are similar to those of *S. retifera*, but are slightly narrower, have less

Figures 35–38. *Scalina deroyae* (DuShane, 1970). Figure 35. LACM 55642, specimen 3. Mexico, Recent. Basal view. Width is 7.1 mm. Figure 36. LACM 55642, specimen 2. Apertural view, body whorl broken. Length is 10.5 mm. Figure 37. LACM 55642, specimen 3. Apertural view. Length is 22.4 mm. Figure 38. LACM 128144, Mexico, Recent. Apertural view. Length is 19.8 mm. Figures 39–44. *Scalina isaacsoni*, sp. nov. Figure 39. UWM 98107, DV 1655-4, syntype. Southern Peru, middle Miocene. Lateral view. Length is 40.7 mm. Figure 40. UWM 98110, DV 1655-3, syntype. Southern Peru, middle Miocene. Abapertural view. Length is 18.6 mm. Figure 41. UWM 98109, DV 1653-1, syntype. Southern Peru, middle Miocene. Oblique basal and apertural view. Width is 11.0 mm. Figure 42. MUSM INV 150, DV 1655-4, syntype. Apertural view, outer lip and columella missing. Length is 29.5 mm. Figure 43. UWM 98107. Oblique view of base. Width is 14.5 mm. Figure 44. MUSM INV 151, DV 1655-3, syntype. Apertural view. Length is 20.1 mm.

Figure 45. *Scalina* aff. *S. isaacsoni*, sp. nov. [= *S. weigandi* (Böse, 1910) of Woodring, 1959, not Böse, 1910 (= *S. ferminiana*)]. USNM 562642, USGS locality 16937, Panama, late Miocene to early Pliocene. Length is 20.4 mm.

Figures 46–48. *Scalina belti*, sp. nov. UWM 98100, DV 575-3, holotype. Southern Peru, late early Miocene. Figure 46. Close-up of sculpture showing medial secondary spiral cords. Figure 47. Lateral view. Length is 23.0 mm. Figure 48. Basal view.

Figures 49–52. *Scalina brophyi*, sp. nov. Figure 49. MUSM INV 148, DV 478-3, paratype. Southern Peru, early Miocene. Abapertural view. Length is 31.8 mm. Figure 50. UWM 98101, DV 478-3, holotype. Apertural view, outer lip missing. Length is 48.6 mm. Figure 51. UWM 98102, DV 478-3, paratype. Lateral view of one whorl. Length is 13.1 mm. Figure 52. UWM 98101. Oblique basal view. Width is 18.0 mm.

Figures 53–55. *Scalina foosei*, sp. nov. UWM 98104, DV 1123-1, holotype. Southern Peru, late Eocene. Figure 53. Basal view. Width is 9.1 mm. Figure 54. Close-up of sculpture. Figure 55. Lateral view. Length is 32.5 mm.

impressed sutures and less tabulate shoulders, more costae per whorl, more uniformly developed primary spiral cords, less well developed secondary spiral cords, and spiral cords that are more differentiated in size on the basal region.

Occurrence: Recent: Mexico to Ecuador.

Scalina isaacsoni, sp. nov.

Figures 39–44

Diagnosis: Shell length to 50 mm. Spire angle 16 to 19 degrees; whorls strongly convex. Sculpture strongly reticulate. Primary spiral cords narrow, elevated, rounded. Secondary cords absent between primary spiral cords.

Description: Shell length to 50 mm. Spire angle 16 to 19 degrees. Whorls strongly convex, slightly angulate posterior to midpoint; sutures deeply impressed; shoulder broad, steeply inclined. Protoconch unknown. Teleoconch of 14 to 15 whorls; sculpture strongly reticulate. Axial sculpture of 34 to 36 weakly scalloped costae on largest body whorls, more costae on earlier whorls. Costae thin, some thickened and standing above spiral sculpture, some slightly extended radially or adapically. Earliest teleoconch whorl posteriorly angulate with spiral formula dCB; subsequent whorls with spiral formulae EDCB, EDCBa, EDCBArr, and on body whorl, usually wEDCBArr, or less often, EDCBAr. Primary spiral cords evenly spaced; interspace between spiral cord 'E' and anterior suture similarly separated; 'B,' 'C,' and 'D' are larger. Spiral cords steeply rounded, elevated, half as wide as interspaces or narrower. Interspaces with reticulation of tertiary spiral and axial threads. Basal disk absent; basal region moderately inclined, planar, with about ten to 14 low secondary spiral cords, intervening tertiary spiral threads, extensions of axial costae, and axial threads; bounded by strong primary spiral cord. Aperture nearly circular, weakly spatulate near columella. Outer lip thin. Umbilicus absent.

Type Locality: DV 1655-4, west face of small ridge, lower Ica valley, 14 m up in measured section, thin sandstones interpreted to be deposited in a large embayment (Figure 56). Pisco Formation. Middle Miocene.

Etymology: Named for Peter E. Isaacson, the author's senior thesis advisor at Amherst College from 1976 to 1977.

Discussion: Specimens of *Scalina isaacsoni* resemble those of the Recent Atlantic *S. retifera* and Pacific *S. deroyae*. Adult specimens of both Recent species, however, are half the length of the largest of *S.*

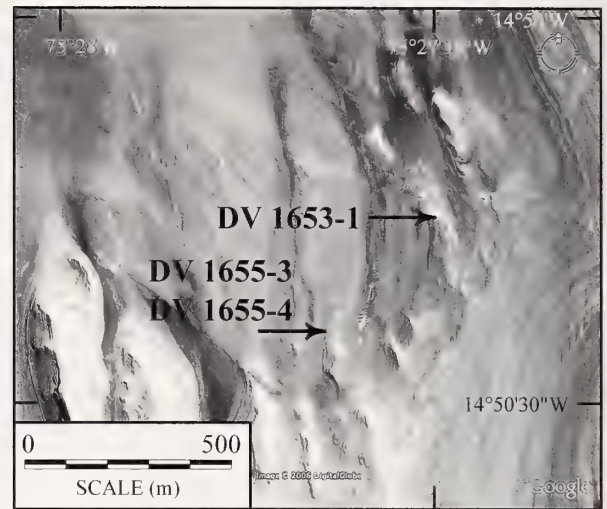


Figure 56. Type locality (DV 1655-4) of *Scalina isaacsoni*, sp. nov., 14 km north-northwest of Puerto Caballas, southern Peru.

isaacsoni, have weaker secondary spiral cords near both sutures or lack such spiral cords, and have axial costae that are more lamellar, recurved, and stand well above the spiral cords. *S. retifera* also has fewer (26 to 27) costae.

Specimens of *Scalina spathe* (Woodring, 1928) from the upper Pliocene Bowden Formation of Jamaica are also smaller than specimens of *S. isaacsoni* and have lamellar recurved costae like those on specimens of *S. retifera*. Specimens assigned to *S. weigandi* (Figure 45) by Woodring (1959) from the upper Miocene or lower Pliocene Chagres sandstone of Panama (Coates et al., 1992; Collins et al., 1996) are as large as specimens of *S. isaacsoni*, similarly sculptured, but have more pronounced and lamellate axial costae; they are morphologically intermediate between specimens of *S. isaacsoni* and the two Recent taxa, *S. deroyae* and *S. retifera*. Specimens of *S. edwilsoni* DuShane, 1977, from the lower to middle Pliocene Tirabuzón Formation of Baja California (Carreño, 1981) have a wider spire angle (about 21 to 22 degrees), lamellar extensions on many costae, and occasionally intercalated secondary spiral cords (e.g., spiral formulae wEDuCBArrr and wEDCBArrr; new photographs of the holotype and a paratype were provided by M. C. Perrilliat, 2006). Fragments of *Scalina* from the middle Pliocene Agueguexquite Formation of southern Mexico (*Scalina* aff. *S. pseudoderoyi*; see Perrilliat, 1972) may be assignable to *S. edwilsoni*.

Specimens of *Scalina isaacsoni* resemble those of the much shorter (<20 mm) and slightly broader (spire angle 19 to 21 degrees) late early Miocene Californian *S. whitei* (Keen, 1943; Addicott, 1970). The spiral formula of the Californian species is close to that of *S.*

isaacsoni (wEDCBarr or WEDCBarr) and for comparable sized whorls the number of costae is similar, but spiral cords of *S. whitei* are wider and secondary spiral cords 'r' are usually more numerous. Specimens of *S. isaacsoni* also resemble the single small specimen of *S. reticulata* Martin, 1904, from the middle Miocene Calvert Cliffs of Maryland (Martin, 1904; Andrews, 1988). The Maryland specimen has spiral cords that are less evenly spaced and intermediate in complexity between *S. isaacsoni* and the pair of late early Miocene species, *S. belti* and *S. kendacensis*.

Material: (all UWBm and MUSM INV specimens are middle Miocene syntypes from Peru) MUSM INV 150, DV 1655-4, L (29.5), W 15.2; MUSM INV 151, DV 1655-3, L 20.1, W 9.3; MUSM INV 152, DV 1655-3, L 16.1, W 5.4; MUSM INV 153, DV 1655-3, L 17.5, W 6.2; UWBm 98107, DV 1655-4, L (40.7), W (14.5); UWBm 98108, DV 1655-4, L (27.3), W 11.7; UWBm 98109, DV 1653-1, L 29.7, W 11.0; UWBm 98110, DV 1655-3, L 18.6, W 6.6; UWBm 98111, DV 1655-3, L 22.6, W 7.6. *Scalina* aff. *S. isaacsoni*: USNM 562641, USGS locality 16937, Panama, late Miocene to early Pliocene, L(26.8), W 14.0; USNM 562642, USGS 16937, L (20.4), W 14.6.

Occurrence: Early middle Miocene: southern Peru.

Scalina belti, sp. nov.

Figures 46–48

Scalina pseudoleroyi (Maury). Jung, 1965, p. 493, pl. 65, fig. 6.

Diagnosis: Spire angle 15 degrees. Interspaces between steeply rounded primary spiral cords with medial secondary spiral cord.

Description: Shell length to 30 mm. Spire angle 15 degrees. Whorls moderately convex, evenly rounded; sutures moderately impressed; shoulder poorly delimited. Protoconch unknown. Spire incomplete; teleoconch with at least six whorls; sculpture moderately reticulate, spiral elements stronger than axial elements. Axial sculpture of 43 evenly spaced thin costae. Costae rarely standing above spiral cords, not extended on shoulder or elsewhere. Spiral formulae wEDCBarr (early whorl) and wEvDuCtBsaRrr (body whorl). Primary spiral cords evenly spaced; 'B,' 'C,' 'D,' and 'E' equally strong. Interspaces between primary spiral cords with medial secondary spiral cord; broad interspace between 'E' and anterior suture. Spiral cords steeply rounded, elevated, half as wide as interspaces or narrower. Interspaces with reticulation of minute tertiary spiral and axial threads. Basal disk absent; basal region moderately inclined, planar, with 12 closely spaced secondary spiral cords, extensions of

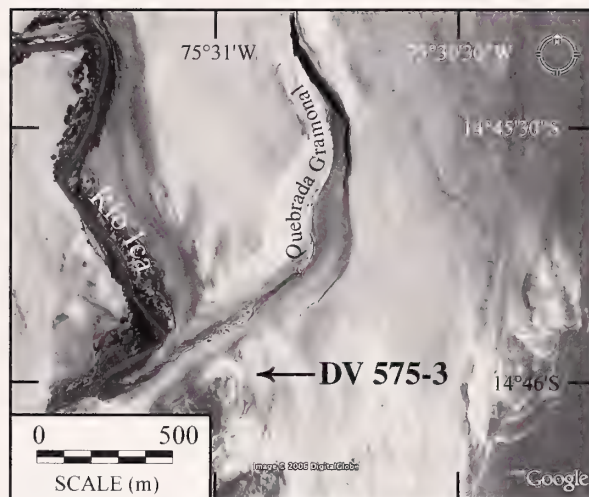


Figure 57. Type locality (DV 575-3) of *Scalina belti*, sp. nov., near juncture of Quebrada Gramonal and the Río Ica, southern Peru.

costae, and tertiary spiral axial threads; bounded by primary spiral cord. Aperture ovate, outer lip and most of columella missing. Umbilicus absent.

Type Locality: DV 575-3, south wall of Quebrada Gramonal near its juncture with the Río Ica, in cross-bedded delta foresets, Chilcatay Formation (Figure 57). Southern Peru, lower Miocene.

Etymology: Named for Edward S. Belt, the author's sedimentology and paleontology professor at Amherst College from 1975 to 1976.

Discussion: Peruvian specimens of the late early Miocene *Scalina belti* differ from those of early middle Miocene *S. isaacsoni* in several respects: they are narrower, they have more numerous but less elevated axial costae, and they have a medial secondary spiral cord between each pair of primary spiral cords. In these features they resemble specimens of *S. kendacensis* Jung, 1971, from the lower to middle Miocene Grand Bay, Belmont, and Carriacou Formations of Carriacou (Jung, 1971; Donovan et al., 2003), which also have medial secondary spiral cords, but the Peruvian specimens have less well developed costae that lack the shoulder extensions seen on the Carriacou species. In this latter respect, as in all others observed, the Peruvian specimens are identical to those from upper lower Miocene beds of the Cantaure Formation (Paraguana Peninsula, northwestern Venezuela) assigned to *S. pseudoleroyi* by Jung (1965). Specimens of *S. belti* differ from those of the slightly older *S. brophyi* of the Pisco Basin by having fewer secondary spiral cords near both sutures and secondary cords that are intercalated medially between much stronger primary spiral cords.

Material: UWBM 98100, DV 575-3, holotype, Peru, early Miocene, L (23.0), W 8.6; MUSM INV 147, DV 575-3, L (7.9), W 6.0; UWBM 98112, Chilcatay Hills, Peru, early Miocene, L (49.8), W (16.9).

Occurrence: Late early Miocene: northwestern Venezuela to southern Peru.

Scalina brophyi, sp. nov.

Figures 49–52

Diagnosis: Shell length to 50 mm. Spire angle 18 degrees. Secondary cords numerous near both sutures, one each between primary spiral cords.

Description: Shell length to 50 mm. Spire angle 18 degrees. Whorls moderately convex, evenly rounded; sutures moderately impressed. Protoconch unknown. Spire incomplete; teleoconch with at least nine whorls. Sculpture reticulate; spiral elements stronger. Axial sculpture of an estimated 50 evenly spaced thin costae, occasionally thickened; rarely lamellar. Costae stand slightly above spiral cords, sometimes extended at suture. Spiral formula wwEvDuCtBsArrrr or wwEvDuCtBsArrrrrr. Primary spiral cords evenly spaced, interspace between 'E' and anterior suture slightly broader; 'B,' 'C,' and 'D' strongest. Anterior primary spiral cords with anterior ramp; posterior spiral cords steeply rounded anteriorly and posteriorly, less than half the width of adjacent interspaces. Interspaces with non-medially situated secondary spiral cords, also with reticulation of minute tertiary spiral and axial threads. Basal disk absent; basal region steeply inclined, planar, with 20 secondary spiral cords, extensions of axial costae, and minute spiral and axial threads; bounded by strong spiral cord. Aperture ovate, poorly preserved. Umbilicus absent.

Type Locality: DV 478-3, Lomas Chilcatay, above orange sandstones of Chilcatay Formation on hillside south of Comotrana-Carhuas road, east of Bahia de la Independencia, southern Peru (Figure 58). Beds represent shoaling episode on outer shelf. Lower Miocene.

Etymology: Named for Gerald P. Brophy, the author's mineralogy professor at Amherst College in 1976.

Discussion: Specimens of *Scalina brophyi* differ from those of younger species in southern Peru by having a greater number of secondary spiral cords between the suture and primary spiral cord 'A,' and from those of all younger species from Peru other than *S. belti* by having intercalated secondary spiral cords between all primary spiral cords. Specimens of the slightly younger *S. belti* have fewer secondary spiral cords near both sutures and the secondary spiral cords are medially situated. Specimens of the Pliocene *S. pseudoleroyi* have

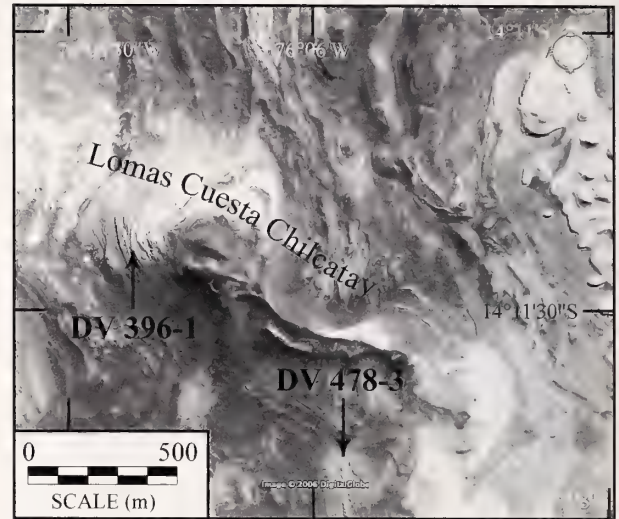


Figure 58. Type locality (DV 478-3) and second locality (DV 396-1) with *Scalina brophyi*, sp. nov., on southwest face of Lomas Cuesta Chilcatay, southern Peru.

wider spire angles and lack intercalated secondary spiral cords.

Material: UWBM 98101, DV 478-3, holotype, Peru, early Miocene, L 48.6, W 18.0; MUSM INV 148, DV 478-3, paratype, L (31.8), W 13.0; UWBM 98102, DV 478-3, paratype, L (13.1), W 9.9; UWBM 98103, DV 396-1, Peru, early Miocene, L (21.8), W 14.0.

Occurrence: Early Miocene: southern Peru.

Scalina foosei, sp. nov.

Figures 53–55

Diagnosis: Spire angle 15 degrees. Teleoconch with eight whorls. Sculpture of weakly rounded primary spiral cords and intervening secondary spiral cords. Basal disk present, not bounded by primary spiral cord.

Description: Shell length about 35 mm. Spire angle 15 degrees. Whorls weakly convex, evenly rounded; sutures weakly to moderately impressed. Protoconch less than two whorls; smooth. Teleoconch with eight whorls. Sculpture weakly reticulate; spiral elements stronger. Axial sculpture of about 75 costae, most regularly spaced, some standing above spiral cords; lamellar near sutures, worn elsewhere. Spiral formula wwwEvDuCtBsARr. Primary spiral cords broadly and symmetrically triangular or weakly rounded. Primary spiral cords unevenly spaced. Interspaces worn, but with hint of tertiary reticulation. Basal disk present, worn, but with trace of secondary spiral cords; not bounded by primary spiral cord. Aperture mostly

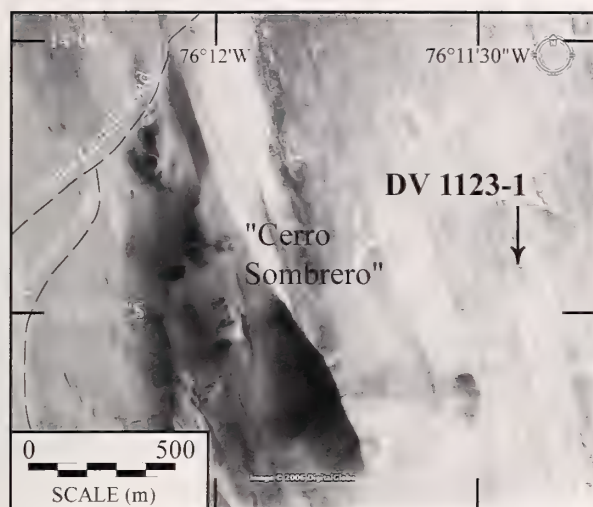


Figure 59. Type locality (DV 1123-1) of *Scalina foosei*, sp. nov., near the informally named Cerro Sombrero, between Laguna Grande and Pozo Santo, southern Peru.

destroyed; ovate, slightly spatulate at columella. Umbilicus absent.

Type Locality: DV 1123-1, southeast corner of informally named Cerro Sombrero in basal sandstones of the Otuma Formation, southern Peru (Figure 59). Late Eocene.

Etymology: Named in memory of Richard M. Foose, the author's professor of introductory geology, oceanography, and structural geology at Amherst College from 1973 to 1976.

Discussion: The sole specimen of *Scalina foosei* was compared with specimens of two Paleogene species of *Scalina* from the northeastern Pacific Ocean, *S. becki* (Durham, 1937) and *S. berthiaumei* (Durham, 1937), as well as figures of other taxa from Oregon and Washington [e.g., *S. aragoensis* (Durham, 1937), *S. dickersoni* (Durham, 1937), *S. lincolnsensis* (Weaver, 1916); see Durham (1937), Weaver (1942), and Hickman (1969)], California [*S. pinolensis* (Clark, 1918); *S. atwoodi* (Dall, 1908), see Dall, 1908b], and Paleogene species from the Gulf Coast of the United States and Mexico [e.g., *S. escandoni* (Gardner, 1945); *S. trigintanaria* (Conrad, 1848) and related taxa (Gardner, 1945; MacNeil & Dockery, 1984); *S. menthafontis* MacNeil, 1984; *S. rubricollis* MacNeil, 1984; and *S. macula* Garvie, 1996]. Western American Paleogene species, including *S. foosei*, usually have retractive costae that merge tangentially with the posterior suture, a character not usually seen on specimens of Neogene species from the eastern Pacific or western Atlantic Ocean or Recent species from any ocean (Weil et al., 1999; but see DuShane's (1977) description of *S. edwilsoni*). Specimens of *Scalina foosei* have well differentiated primary

and secondary spiral cords not seen on specimens of other Paleogene species of *Scalina* from the Pacific Northwest or Gulf Coast of the U.S and Mexico, excepting *S. trigintanaria hopkinsi* MacNeil, 1984, a species from the lower Oligocene Mint Spring Formation of the southeastern United States (Pettway & Dunn, 1990).

Material: (all specimens from Peru, late Eocene): UWM 98104, DV 1123-1, holotype, L 32.5, W 9.1; MUSM INV 149, DV 1220-1, L (12.7), W (7.8); UWM 98105, DV 631-8, L (16.6), W 6.7.

Occurrence: Late Eocene: southern Peru.

DISCUSSION

Not all identifications of *Scalina* stand up to close scrutiny. A specimen of *Scalina whitei* (Keen, 1943) from lower Miocene strata on King George Island, near Antarctica (Karczewski, 1987) is an incorrectly identified, poorly preserved mold with some surface sculpture intact. The Californian Paleogene *Acrilla* (*Ferminoscala*) *durhami* Zinsmeister, 1983, has prominent spiral nodes and therefore is not a member of *Scalina*; it should also not be confused with *Ferminoscala durhami* Keen, 1943, which is herein considered a junior synonym of *S. whitei*. Specimens of the Californian Pleistocene *Scalina effiae* (Willet, 1939), described and figured by DuShane (1979), have fine spiral scratches unlike any seen on other specimens of *Scalina*, obscure spiral cords beneath the surface shell layer, and little difference between spiral sculpture above and below a faint basal spiral cord.

The epitoniid, *Scala* (*Acrilla*) *pompholyx* Dall, 1890, known only from a single specimen (*vide* DuShane, 1974) collected off the Galapagos Islands at a water depth of 1485 m, differs in so many characters from the suite of Cenozoic *Scalina* species in the Americas that its assignment to the subgenus is doubtful.

Paleogene comparisons

The late Eocene epitoniid from southern Peru, *Scalina foosei*, has costae that are retractive at the posterior suture like those on many Paleogene species from North America. Specimens of Paleogene species from California, Oregon and Washington, however, have numerous equally developed primary spiral cords with few if any secondary spiral cords, as do most Paleogene species from the Gulf Coast of Mexico and the United States. The differentiation of primary and secondary spiral cords on the specimen of *S. foosei* is more like that seen on lower Oligocene Gulf Coast specimens of *S. trigintanaria hopkinsi* and specimens of the early Miocene Peruvian species, *S. brophyi*. De-

ciding if this similarity reflects a close phylogenetic relationship between *S. foosei* and the latter two species awaits the discovery of more Paleogene material from Central and South America.

The 'brophyi' and nested 'isaacsoni' clades

The 'brophyi' clade includes all Neogene American species of *Scalina*. These species differ from most Paleogene species by having steeply rounded spiral cords and costae that are not retractive at the posterior suture and are distinguished from most modern non-American taxa by a pattern of spiral ornamentation (spiral formula wEvDuCtBsAr or some variant) together with secondary spiral cords, that, if present, are generally much smaller than the primary spiral cords. Nested within the 'brophyi' clade is an 'isaacsoni' clade, which is characterized by strong primary spiral cords, greatly reduced secondary spiral sculpture, and increasingly lamellar costae that may stand well above the spiral cords.

Specimens of the oldest Neogene American species, *Scalina brophyi*, collected from southern Peru in strata of 23 to 19 Ma (DeVries, 1998), have anterior ramping of some spiral cords and numerous secondary spiral cords. The 17-Ma Peruvian and Venezuelan species, *S. belti*, the nearly identical early to middle Miocene eastern Caribbean *S. kendacensis*, and the less elongate early to middle Miocene southern Californian *S. whitei* more closely resemble *S. retifera*; they have a single intercalated secondary spiral cords between the primary spiral cords and fewer secondary spiral cords adjacent to the anterior and posterior sutures.

The oldest species in the nested 'isaacsoni' clade and the youngest species of *Scalina* from southern Peru is the middle Miocene *S. isaacsoni* (about 14 to 13 Ma; DeVries, 1998). Specimens of this species exhibit a further tendency towards reduced secondary spiral sculpture. Specimens have two 'r' secondary spiral cords adjacent to the posterior suture, an 'w' secondary spiral cord near the anterior suture, and no intercalated secondary spiral cords.

Late Miocene and Pliocene species of the 'isaacsoni' clade include the early to middle Pliocene *Scalina edwilsoni* from Baja California, and in the Atlantic Ocean, the late Miocene to Pliocene *Scalina weigandi* (*sensu* Woodring, 1959) from Panama and the late Pliocene *S. spathe* from Jamaica. The 'isaacsoni' clade culminates with two Recent geminate species, the Pacific *S. deroyae* and Atlantic *S. retifera*, both of which have minimal secondary spiral sculpture. Together, the two Recent species occupy the range formerly inhabited by late Neogene taxa, except that *S. retifera* also ranges to Brazil and West Africa (Weil et al., 1999), whereas *S. deroyae* presently ranges no farther south than Ecuador (DuShane, 1970, 1974).

The 'cheneyi' clade

The oldest evidence in southern Peru of a departure from the strongly reticulate sculpture of the early Miocene species of the 'brophyi' clade and the more widely distributed middle Miocene-to-Recent 'isaacsoni' clade is the appearance of *S. cheneyi* in upper Miocene beds in southern Peru (about 9 Ma; Muizon & DeVries, 1985; DeVries, 1998). Specimens of *S. cheneyi* have primary spiral cords that are broader and lower than those of species from either ancestral taxa or taxa of the sister 'isaacsoni' clade; costae are weaker, secondary spiral cords are less numerous, a true basal disk is present, and the spire angle is wider. The oldest late Miocene specimens of *S. cheneyi* are small; younger late Miocene and early Pliocene specimens are as large as those of any older Peruvian species.

The 'pseudoleroyi' clade

Even larger than specimens of *Scalina cheneyi* and with a wider spire angle, anteriorly ramped primary spiral cords, and prominent tertiary threads overrunning the primary spiral cords, are specimens of the 'pseudoleroyi' clade, which lies nested within the 'cheneyi' clade and appeared in early Pliocene Caribbean waters as *Scalina pseudoleroyi*. The most widely distributed of the 'pseudoleroyi' taxa is *S. ferminiana*, which lived during the late Pliocene in the Pacific [northern Peru (DeVries, 1986), Ecuador (Pilsbry & Olsson, 1941; DuShane, 1988)] and Atlantic Ocean [*S. weigandi* (Böse, 1910) (= *S. ferminiana*), eastern side of the Isthmus of Tehuantepec, Mexico], but today is restricted to the Pacific Ocean. The appearance of this species on both sides of Central America, as well as the presence of the similar *S. mitchelli* in the Gulf of Mexico, indicates that populations of the 'pseudoleroyi' clade had become established in both the Pacific and Atlantic Ocean before the closure of the Isthmus of Panama.

The 'brunneopicta' clade

Elongate epitoniids with broad, flattened spiral cords and partly formed basal disks appear in the late Miocene in Panama (Woodring, 1959) and Pliocene in Ecuador (Pilsbry & Olsson, 1941) and have persisted until the present in the tropical eastern Pacific Ocean as *Scalina brunneopicta*. The spiral sculpture on these specimens resembles that of the less elongate, more convexly formed specimens of the Peruvian late Miocene *S. cheneyi*.

Phylogenetic summary of Neogene *Scalina* in the Americas

A stratigraphy-based phylogeny of American taxa of *Scalina* is presented in Figure 60. Species are arranged

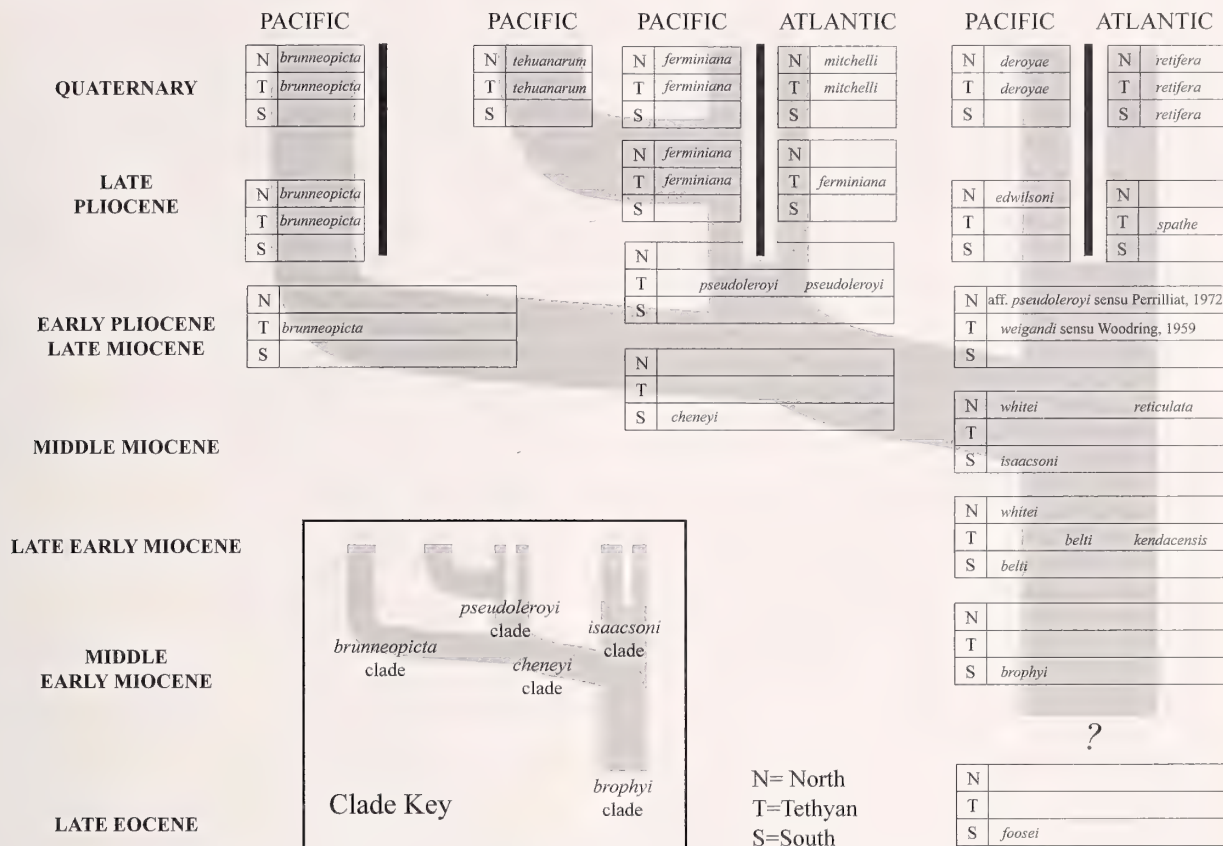


Figure 60. Proposed Neogene phylogeny of American species of *Scalina*. Species are placed according to age and geography (T = equatorial Tethyan realm; N = boreal tropical and subtropical latitudes; S = austral tropical and subtropical latitudes). Black vertical bars represent the separation of the Atlantic Ocean from the Pacific Ocean following the closure of the Isthmus of Panama. Clades of *Scalina* species are named at lower left.

according to their distribution north (N) and south (S) of a narrow Tethyan-equatorial region (T) and according to their geochronological range. No claim is made that one of the listed species is the direct ancestor or descendant of another so listed. Rather, the overlay of a phylogenetic tree on the Recent and fossil taxa shows a pattern of evolution, with the understanding that specific taxa may have evolved from a region or species in the Americas not yet represented in the figure.

Species of *Scalina* ranged from the Pacific Northwest of the United States to southern Peru and throughout the Gulf of Mexico during the Eocene and early to middle Oligocene. By the early Miocene, species of *Scalina* had disappeared from higher northern latitudes. Through much of the remainder of the Miocene, species of the 'isaacsoni' clade occupied American waters, albeit in lower latitudes by the late Miocene. During the late Miocene, a diversification within American *Scalina* yielded two new clades exemplified by the Recent *S. ferminiana* and *S. brunneopicta*. The evolutionary radiation, whose earliest manifestations

were *S. cheneyi* (Peru) and *Scalina* cf. *S. brunneopicta* (Panama), preceded the closure of the Isthmus of Panama by several million years (Coates et al., 1992).

In southern Peru, *Scalina* did not undergo the evolutionary radiation during the late Pliocene that was experienced by endemic taxa (DeVries, 2001). Rather, when sea-surface temperatures began to decline but before the Peruvian coast commenced a late Pliocene uplift, *Scalina cheneyi* disappeared from southern Peru, ending a 30 million year presence of *Scalina* in those austral waters. The local extinction of *Scalina* in southern Peru coincided with the local or complete extinction of other taxa with equatorial affinities in southern Peru (DeVries, 2001).

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Appendix Locality-Samples

ANSP 13640	Punta Blanca, Manabi Province, Ecuador. Pliocene.
ANSP 13641	Punta Blanca, Manabi Province, Ecuador. Pliocene.
DV 236-3	Three km south of the village of El Nuro, one km north of Cerro El Nuro, northern Peru. Cliff edge, Mancora Tablazo, lower part of section, on knoll below Mancora Tablazo surface, just below and north of gravel service road which proceeds from valley floor to tablazo surface; northwest corner of tablazo cliff face. [Description from 1981 (DeVries, 1986)]. Taime Formation, upper Pliocene.
DV 267-3	South face of Quebrada Carmen, three km south-southeast of El Alto, northern Peru. Taime Formation, upper Pliocene.
DV 396-1, 478-3	Lomas Chilcatay, southern Peru, orange sandstones between whitish tuffaceous fine sandstones. About 14°11'50"S, 76°06'00"W. Punta Grande 1:100,000 quadrangle. Chilcatay Formation, lower Miocene.
DV 523-2	Cerro Terrestrial, southern Peru, near top of section. 14°48'02"S, 75°23'02"W. Palpa 1:100,000 quadrangle. Pisco Formation, upper Miocene to lower Pliocene.
DV 523-4	Cerro Terrestrial, southern Peru, just below reddish beds in section. 14°48'02"S, 75°23'02"W. Palpa 1:100,000 quadrangle. Pisco Formation, upper Miocene to lower Pliocene.
DV 571-6	Alto Grande (El Jahuay of Muizon & DeVries, 1985), southern Peru. Near top of hill, west side of Panamerican Highway, shell beds across hillside. 15°26'57"S, 74°52'06"W. Acari 1:100,000 quadrangle. Pisco Formation, upper Miocene.
DV 575-3	Quebrada Gramonal, southern Peru; south wall, near juncture with the Río Ica. 14°45'40"S, 75°30'47"W. Lomitas 1:100,000 quadrangle. Chilcatay Formation, lower Miocene.
DV 599-2	Montemar, Sacaco Basin, southern Peru. Yauca 1:100,000 quadrangle. Pisco Formation, upper Miocene.
DV 631-8	Northwest of Loma Cuesta Chilcatay, southern Peru; continuous outcrop of sandstone below Chilcatay formation near Carhuas-Comotrana road. Fault slices with basement brought up on east side of main valley. 120.5 m in measured section. Punta Grande 1:100,000 quadrangle. Otuma Formation, upper Eocene.
DV 1123-1	Southeast corner of informally named Cerro Sombrero, basal yellow-white indurated sandstones on lower eastern side of small valley. 14°06'25"S, 76°11'08"W. GPS. Punta Grande 1:100,000 quadrangle. Otuma Formation, upper Eocene.
DV 1348-1	East side of Montemar, near Panamerican Highway. 15°31'18"S, 74°48'57"W. GPS. Yauca 1:100,000 quadrangle. Pisco Formation, late Miocene.
DV 1653-1	Nose of next to easternmost wind-carved north-south ridges east of the lowermost Río Ica and 'Labyrinth' zone; 'Sula' site of Stucchi fossil bird localities. Basal lagoonal sandstones. 14°50'16"S, 75°27'30"W. GPS. Lomitas 1:100,000 quadrangle. Pisco Formation, lower middle Miocene.
DV 1655-3	Southwest of 'Sula' site (DV 1653-1) by 400 m; shelly ridge in basal sandstones on west face of long ridge. 14 m above base of formation. 14°50'26"S, 75°27'38"W. GPS. Lomitas 1:100,000 quadrangle. Pisco Formation, lower middle Miocene.
DV 1655-4	Southwest of 'Sula' site (DV 1653-1) by 400 m; shelly ridge in basal sandstones on west face of long ridge. 16 m above base of formation. 14°50'26"S, 75°27'38"W. GPS. Lomitas 1:100,000 quadrangle. Pisco Formation, lower middle Miocene.
DeVries collection	<i>Scalina retifera</i> : Isla Escudo de Veraguas, Panama (Caribbean), dedged at 120 m water depth. Recent.
FMNH 145466	Yucatan, Mexico, off Campeche Banks, 40 m water depth. Recent.
FMNH 152778	Yucatan, Mexico, off Campeche Banks, 30 m water depth. Recent.
FMNH 00128594	Freeport, Texas. Recent.
LACM 1162	Gulf of Tehuantepec, Mexico, 59–68 m on mud bottom. 15°58'N, 95°00'W. Recent.
LACM 1236	(= AHF 147-34) Tagus Cove, Albermarle Island, Galapagos Islands, Ecuador, at 54 m water depth, on rock and coral. 0°16'38"S, 91°22'44"W. Recent.

Appendix
Continued.

LACM 127965	Guaymas, Sonora, Mexico, collected by shrimpers. Recent.
LACM 128144	Southeast of San Antonio Point, Guaymas, Sonora, Mexico, at 90 m water depth. Recent.
LACM 164927	Off Egmont Key, Pinellas County, Florida, at 121.9 m water depth. Recent.
LACM 38-8	Sihuantanejo, Guerrero, Mexico, at 36–73 m water depth. 17°38'N, 101°34'W. Recent.
LACM 55642	Southeast of San Antonio Point, Guaymas, Sonora, Mexico, at 90 m water depth. Recent.
LACMIP 11794	Onzole Formation, Esmeraldas Province, Ecuador. Pliocene.
PRI 4065	Charco Azul, Panama. Pliocene.
USGS 8410	Cuts on north (west) side of French Canal (East Diversion), Mount Hope, Canal Zone, Panama. Pliocene.
USGS 16937	Caribbean coast of Panama near mouth of Río Piña; road cut on west side of river about 90 m west of road fork. Massive fine-grained sandstone. Upper Miocene to lower Pliocene.
UCMP B1601	Coarse gravelly sand, east of hill 933. Caliente quadrangle, California. Upper part of Olcese Sand. Middle Miocene.
UCMP B1638	Caliente quadrangle, California. Lower part of Round Mountain Silt. Middle Miocene.
USGS 6064	North of Kern River, 11 miles southeast of Bakersfield, California. Lower part of Round Mountain Silt. Middle Miocene.
USGS M1608	South bank of Kern River. Rio Bravo Ranch quadrangle, California. Lower part of Round Mountain Silt. Middle Miocene.
USGS M1613	Rio Bravo Ranch quadrangle, California. Lower part of Round Mountain Silt. Middle Miocene.
USGS M2480	About 12 m stratigraphically above USGS M1613. Rio Bravo Ranch quadrangle, California. Lower part of Round Mountain Silt. Middle Miocene.

The First *Alora* H. Adams, 1861 (Gastropoda: Epitoniidae) from Western South America: Unique Miocene Records

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Abstract. *Alora teresmonile*, sp. nov., from middle and upper Miocene beds of the Pisco Basin in southern Peru is the first epitoniid of its genus to be found in western South America and the first fossil species of *Alora* from anywhere. A Miocene Tethyan distribution probably accounts for the pattern of widely separated Recent *Alora* taxa. In southern Peru, *A. teresmonile* first appeared as part of an evolutionarily transitional molluscan fauna living in a coastal upwelling regime during a time of globally decreasing sea surface temperatures.

INTRODUCTION

Alora H. Adams, 1861, includes small, thin-shelled, often globose epitoniids with spiral and axial sculpture (Keen, 1969; DuShane, 1974; Weil et al., 1999; Nakayama, 2003). Extant species have been reported from Panama and Mexico [*A. gouldii* (A. Adams, 1857); *A. billeeana* (DuShane & Bratcher, 1965)], southeast Asia [*A. annulata* (Kuroda & Ito, 1961)], Japan [*A. annulata*; *A. kiiensis* Nakayama, 2000; *A. reticulata* (Habe, 1962)], the North Atlantic Ocean [*A. retifera* Bouchet & Warén, 1986; *A. tenerrima* (Dautzenberg & Fischer, 1896)], Brazil [*A. retifera* (S. Vanin, personal communication, 2007; <http://www.conchas-brasil.org.br>, March, 2007)], and East Africa (*A. rapunculus* Kilburn, 1975). A single fossil species has been identified, the Miocene *A. minihagali* (Deraniyagala, 1956) from Sri Lanka (Neville, 1997).

This paper reports the first *Alora* of any age from western South America, contradicts the assignment of the Sri Lankan Miocene species to *Alora*, and briefly addresses the biogeographic implications of Miocene *Alora* from southern Peru.

GEOLOGY

The stratigraphy of the Cenozoic Pisco Basin in southern Peru has been described by DeVries (1998). The older specimens of *Alora* were found in the lower third of the Pisco Formation in the Río Ica valley. The presence of the gastropods *Testallium cepa* (Sowerby, 1846), *Concholepas unguis* DeVries, 1995, and *Acanthina katzi* Fleming, 1972, in the same sandstone beds as *Alora* confirms an early to early middle Miocene age for the epitoniid species (DeVries, 1995, 2003; DeVries & Schrader, 1997; Vermeij & DeVries, 1997), an age further constrained to the middle Miocene by the co-occurrence of *Turritella infracar-*

inata Gryzbowski, 1899 (DeVries, 2007). The younger specimens of *Alora* were found in tuffaceous beds of the Pisco Formation in the smaller Sacaco Basin at Aguada de Lomas. The base of the Aguada de Lomas section is dated by ⁴⁰K–⁴⁰Ar at about 9 to 8 Ma, whereas the upper part of the section lies below a very late Miocene unconformity (Muizon & DeVries, 1985), thereby suggesting an age of about 7–6 Ma for the *Alora* specimens.

MATERIALS AND METHODS

Fossils described in this study were found by the author. Measurements of length (L) and width (W) are in millimeters; those enclosed by parentheses indicate sizes for broken or deformed specimens.

Abbreviations for depositories for fossil specimens are as follows: MUSM INV – Departamento de Paleontología de Vertebrados, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; UWBM – Burke Museum of Natural History and Culture, University of Washington, Seattle, USA.

SYSTEMATIC PALEONTOLOGY

Family Epitoniidae S. S. Berry, 1910

Alora H. Adams, 1861

Type species: (by monotypy) *Trichotropis gouldii* A. Adams, 1857.

Teramachiacirsa Kuroda & Ito, 1961, p. 263.

Discussion: *Alora* H. Adams, 1861, was created by Adams for his brother's recently described species, "*Trichotropis gouldii*" A. Adams, 1857. H. Adams (1861) noted the absence of a trichotropine siphonal canal on the '*gouldii*' specimen. Keen (1969) recommended the transfer of *Alora* from Janthinidae to

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Figures 1–9. *Alora teresmonile*, sp. nov. DV 1021-3, southern Peru, middle Miocene. All but UWBM 98113 are paratypes. Figure 1. UWBM 98113, holotype, apertural view. Length is 10.7 mm. Figure 2. UWBM 98113, oblique basal view. Width is 6.0 mm. Figure 3. UWBM 98114, apertural view. Length is 9.6 mm. Figure 4. MUSM INV 154, abapertural view. Length is 10.9 mm. Figure 5. MUSM INV 155, abapertural view. Length is 10.0 mm. Figure 6. UWBM 98114, oblique basal view showing tiny umbilicus. Width is 4.1 mm. Figure 7. MUSM INV 156, lateral view. Length is 11.1 mm. Figure 8. UWBM 98113, protoconch and early spire whorls. Visible length is 1.3 mm. Figure 9. UWBM 98113, protoconch and early spire whorls. Note smooth shoulder of later whorls.

Epitoniidae and further noted the synonymy of *Rechuzia insignis* Pilsbry & Lowe, 1932, with *A. gouldii*.

The type species of *Alora* and other Recent Pacific species, notably *A. billeeana* and *A. reticulata*, have pronounced cancellate sculpture. Other species, including *A. annulata*, *A. rapunculus*, and *A. kiiensis*, have subdued axial costae and well developed spiral cords.

Alora teresmonile, sp. nov.

Figures 1–9

Diagnosis: Up to 50 spiral cords on body whorl of adult specimens, interspaces on earlier whorls having become new spiral cords; cords more widely spaced or absent on shoulder. Axial sculpture obsolete.

Description: Very thin-shelled; shell length to 37 mm. Spire angle variable, as little as 16 degrees, usually 22 to 25 degrees, late Miocene specimens 30 to 40 degrees. Whorls convex to globose, evenly rounded; sutures impressed. Protoconch conical with two smooth whorls. Teleoconch of about six to seven whorls. Axial sculpture of numerous irregularly spaced orthocline to slightly prosocline growth lines, some strengthened to

form weak axial costae, especially on early whorls; some growth lines variably sinuous in response to growth breaks. Spiral sculpture of eight to nine evenly spaced, sharply rounded spiral cords visible on spire whorls, often becoming wider and more widely spaced or obsolete on shoulder. Interspaces become secondary or primary spiral cords on penultimate and ultimate whorls, resulting in about 40 to 50 low rounded spiral cords on body whorl between base and posterior suture; spiral cords closely spaced anteriorly, often widely spaced or obsolete on shoulder. Aperture ovate, strongly spatulate posteriorly to form a pseudosiphonal canal. Outer lip thin. Inner lip not continuous; columella slightly thickened, vertical to arcuate, reflected at anterior end, inclined adaperturally to merge with apertural floor. Umbilicus absent or slightly open.

Type Locality: Locality-sample DV 1021-3, hillside on the east side of Quebrada Gramonal, in lagoonal sandstone lag deposits, lower Pisco Formation, Ica Valley, southern Peru (Figure 10). Middle Miocene.

Discussion: Specimens of *Alora teresmonile* share with specimens of other species of *Alora* a very thin shell, a reflected and adaperturally slanted columella, and markedly convex whorls. Most middle Miocene speci-

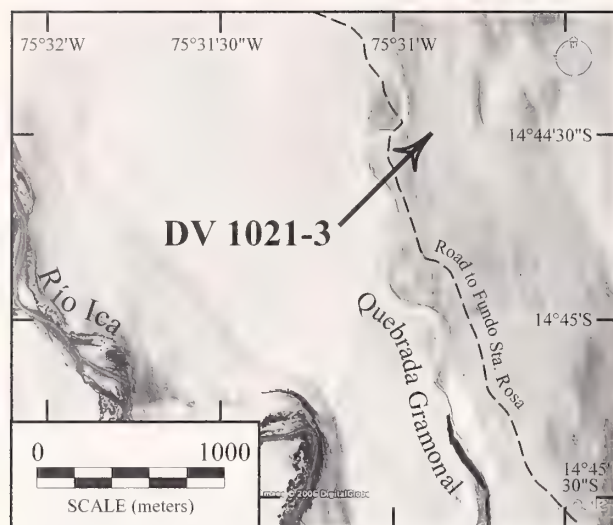


Figure 10. Type locality (DV 1021-3) of *Alora teresmonile*, sp. nov.

mens of *A. teresmonile* have spire angles comparable to those of specimens of *A. gouldii* and *A. kiiensis*; late Miocene specimens have spire angles more like those of the globose *A. annulata* and *A. rapunculus*. Three modes in the distribution in Peruvian spire angles in middle and late Miocene specimens might indicate the existence of three species, but too few examples have been collected to presently justify such a distinction.

Middle Miocene specimens of *Alora teresmonile* are found in coarse-grained sandstones thought to represent lag deposits covering the floor of lagoons and scour-and-fill deposits that may represent the ebb and flood channels to the lagoons. These sandstones and intervening finer-grained sandstones contain a diverse molluscan fauna as well as rare fragments of crinoids and partial or whole skeletons of mysticete whales and *Isurus* sharks. The late Miocene specimens are found in a sequence of massive, bioturbated, and cross-bedded sandstones with intercalated horizons of *Mulinia* bivalves, oysters, and erosive disconformities with pebbles and pumice fragments, all deposited in the lee of a paleo-island composed of pre-Cenozoic igneous rock (Muizon & DeVries, 1985). The inferred shallow depths of these late and middle Miocene *Alora* habitats contrast with the deep-water habitat of some modern *Alora* taxa [e.g., *A. annulata*, 100–300 m water depth (DeVries, collection); *A. retifera*, 1250 m water depth (Bouchet & Warén, 1986); *A. tenerrima*, 1385 m water depth (Dautzenberg & Fischer, 1896)], but are comparable to the shallow waters presently inhabited by individuals of *A. gouldii* and *A. billeeana* in Panama and the Gulf of California (Hinojosa-Arango & Riosmena-Rodríguez, 2004) and *A. reticulata* in Japan (Nakayama, 2003).

Etymology: ‘teres,’ Latin adjective for ‘smooth,’ and ‘monile,’ Latin noun for ‘collar’ or ‘necklace,’ referring to the diminishment of spiral sculpture close to the posterior suture of each whorl.

Material: UWBM 98113, DV 1021-3, middle Miocene, holotype, L 10.7, W 6.0; MUSM INV 154, DV 1021-3, paratype, L (10.9), W 5.4; MUSM INV 155, DV 1021-3, paratype, L (10.0), W 5.8; MUSM INV 156, DV 1021-3, paratype, L 11.1, W 6.0; MUSM INV 157, DV 1021-3, paratype, L 4.9, W 2.4; MUSM INV 158, DV 1655-4, middle Miocene, L 14.7, W 7.5; MUSM INV 161, DV 563-1, late Miocene, L (31.9), W 19.1; MUSM INV 162, DV 563-1, L 16.6, W 10.0; UWBM 98114, DV 1021-3, paratype, L 9.6, W 4.1; UWBM 98115, DV 1655-4, L 22.5, W (10.5); UWBM 98116, DV 1307-1, middle Miocene, L 9.3, W 5.1; UWBM 98207, DV 563-1, late Miocene, L 36.5, W 20.1; UWBM 98208, DV 563-1, L (19.0), W 11.9; UWBM 98209, DV 563-1, L 17.3, W 9.6. DeVries collection, DV 1021-3, lot of 8.

Occurrence: Middle to late Miocene: southern Peru.

DISCUSSION

Alora teresmonile is ostensibly the second fossil species of *Alora*. Efforts to examine material of the only other reported fossil species of *Alora*, the Miocene *A. minihagali*, were unsuccessful; the type specimen has been lost from the National Museum of Natural History in Colombo, Sri Lanka (K. Manamendra-Arachchi, *vide* R. Pethiyagoda, personal communication, March, 2007). A description and figure of the type specimen (Spoila Zeylanica 28(1):3, pl. 2, fig. 2c; 1956) call attention to strong and broad axial ribs, about 14 in number, that are not consistent with Neville’s (1997) assignment of the species to the weakly and finely cancellate *Alora*; Neville (personal communication, April, 2007) is now of the same opinion. Thus, with the Sri Lankan species removed from *Alora*, the Peruvian species constitutes the only documented fossil example of the genus.

Recent species of *Alora* are widely scattered throughout the world’s oceans in shallow and deep water at tropical and subtropical latitudes, probably indicating an equally widespread ancestral distribution with dispersal aided by circumtropical Tethyan circulation. The ease of dispersal for some *Alora* species is demonstrated by the modern pan-Atlantic distribution of *A. retifera* and pan-Pacific distribution of *A. billeeana* (Okutani, 2000; Nakayama, 2003). Given the close association of epitoniids with their coelenterate hosts, the dispersal of *Alora* taxa probably reflects the dispersal capacity of those hosts.

Alora appeared in the Pisco Basin at the same time that other taxa (e.g., *Turritella infracarinata*) arrived from northern Peru and Ecuador (DeVries, 2007). The

middle Miocene was a time of faunal disruption in southern Peru, when global sea surface temperatures were decreasing and when a molluscan fauna that had persisted in southern Peru since the latest Oligocene was being replaced by the antecedents of the 'modern' fauna of the Peruvian Faunal Province (DeVries, 2002). This limited invasion from the north was repeated near the end of the Pliocene under similar climatic and oceanographic circumstances (DeVries, 2002).

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Appendix

Locality-samples

DV 653-1	Northeast corner of Aguada de Lomas, northern Sacaco Basin, at 87 m in measured section, probably equivalent to 180 m in measured section of DV 562-1. 15°28'49"S, 74°48'19"W (Acari 1:100,000 quadrangle). Pisco Formation, upper Miocene.
DV 1021-3	Hillside on the east side of Quebrada Gramonal, in lagoonal sandstone lag deposits, Ica Valley, southern Peru. 14°44'19"S, 75°31'02"W (Lomitas 1:100,000 quadrangle). Lower Pisco Formation, middle Miocene.
DV 1307-1	East of mouth of Quebrada Gramonal, three-meter wide channel-fill bioclastic deposit, 14°45'48"S, 75°30'23"W (Lomitas 1:100,000 quadrangle). Lower Pisco Formation, middle Miocene.
DV 1655-4	East of 'labyrinth' dune field, east of lower reach of Río Ica, 14°50'16"S, 75°27'29"W (Lomitas 1:100,000 quadrangle). Lower Pisco Formation, middle Miocene.

Genera of American Strombid Gastropods (Gastropoda: Strombidae) and Remarks on Their Phylogeny

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Abstract. *Persististrombus* gen. nov. is created to accommodate a number of fossil and one Recent species which form a distinct lineage starting in Early Oligocene of Europe with *Strombus radix* Brongniart, 1823, via the Oligocene to early Miocene *S. bonellii sensu stricto* Brongniart, 1823 and a number of Caribbean extinct species to the Recent Panamic faunal province *Strombus granulosus*. The genus level name *Lobatus* Iredale, 1921 (type species *bituberculatus* Lamarck, 1822) is available. Possible relationships between *Persististrombus* gen. nov. and other Caribbean and Panamic Strombidae are discussed but remain uncertain as the phylogeny of these species is not fully elucidated. Putative evolutionary scenarios are briefly considered.

Gastropoda, Strombidae, new genus, *Persististrombus*, *Lobatus*, phylogeny

INTRODUCTION

The discovery of aberrant specimens of the well known *Strombus granulosus* Swainson, 1821 from the Islas Galápagos and Isla del Coco discussed by Kronenberg & Lee (2004) combined with an earlier paper by Lozouet & Maestrati (1986) compelled the authors to further investigate the relationships of this species and the fossil record of its relatives.

Strombus granulosus was assigned to *Lentigo* Jousseaume, 1886 by Abbott (1960), and this allocation was followed by subsequent workers like Walls (1980), Kronenberg and Berkhout (1984), and DeTurck *et al.* (1999).

As indicated before (Kronenberg & Vermeij, 2002), the lines between subgenera as recognized by Abbott (1960) are rather blurred and arbitrary. *Lentigo*, to which Abbott (1960) assigned five species, viz. *Strombus lentiginosus* Linnaeus, 1758 (type species TS); *S. pipus* (Röding, 1798); *S. fasciatus* Born, 1778; *S. latus* Gmelin, 1791; and *S. granulosus*, is an example of this problem. On the basis of shell characters there are at least three supraspecific taxa included in this group. Moolenbeek & Dekker (1993) have already allocated *S. fasciatus* to *Conomurex* Fischer, 1884 based on shell morphology and characters of the radula. Subsequently, DeTurck *et al.* (1999) replaced it in *Lentigo* without comment. Kronenberg & Vermeij (2002) indicated that both *Strombus granulosus* and *S. latus* differed in a number of conchological characters from the Indo-

Pacific *Lentigo lentiginosus* and *L. pipus*. More recently it has been demonstrated, based on anatomical characters (Simone, 2004) and molecular sequence data (Latiolais, 2003 and Latiolais *et al.*, 2006), that the genus *Strombus sensu* Abbott is not monophyletic.

Sacco (1893:12) was the first to recognize a lineage from the fossil *S. radix* Brongniart, 1823 and *S. bonellii* Brongniart, 1823, for which *Strombus nodosus* (Borson, 1820) might be an earlier name, see Sacco (1893:4) of the Recent *S. granulosus*, an opinion followed by Lozouet and Maestrati (1986). This was acknowledged by Jung & Heitz (2001), who described a number of fossil species, allocating those to *Lentigo*. They also included the Recent *Strombus raninus* Gmelin, 1791, a species previously assigned to *Tricornis* Jousseaume, 1886 or, more recently, to *Lobatus* Iredale, 1921 (Petuch, 1994).

Consistent with reasoning of Kronenberg & Vermeij (2002) and data presented by Latiolais (2003), Simone (2004), and Latiolais *et al.* (2006), and to accommodate the lineage of the Early Oligocene species of Europe and a number of fossil species described by Jung & Heitz (2001) to the Recent *S. granulosus*, a new genus is described herein. As Jung & Heitz (2001) argued that the name *Lobatus* Iredale, 1921 is unavailable, we discuss the nomenclatorial status of that taxon. A review of the literature for possible relationships between the new genus described herein and other strombid genera revealed that there is a number of possible relationships between the Recent Western

Atlantic and Panamic Province fauna and fossil species known from the Early Oligocene to Early Miocene of Europe. These are discussed briefly.

Strombus albirupianus Dall, 1890, described from the Late Eocene (Jackson) white limestone overlying the Claiborne sands, Claiborne Bluff, Alabama, does not appear to be closely related to this lineage judging from the description and figures by Dall (1890:174–175, pl. 12 figs. 2, 10) and is not considered here.

Likewise, two other American fossil strombid species, *S. liocychus* Dall, 1915 from the Miocene Tampa silex beds, Ballast Point, Tampa Bay (Florida, USA) [*cf.* Boss *et al.*, 1968] and *S. leurus* Woodring, 1928 from the Pliocene Bowden Formation of Jamaica are not discussed here as they apparently left no Recent descendants in the Americas. *Strombus liocychus* was allocated to *Canarium* Schumacher, 1817 by Abbott (1960:63). *Strombus leurus* was not discussed by Abbott, but the species bears a strong resemblance to species allocated to *Dolomena* Wenz, 1940 [*Dolomena* Iredale, 1931 is not available; see Kronenberg & Dharma, 2005 and references therein] (Woodring, 1928:326–327; pl. 24, figs. 3–5).

Another possible clade, consisting of the genus *Orthaulax* Gabb, 1873 (*O. inornatus* Gabb, 1873), known from the lowermost middle Eocene of Italy (*O. dainellii* Savazzi, 1989) with a number of Oligocene and Miocene species in America (see Vokes & Vokes, 1968 for a review and discussion) is not discussed herein as we think that *Orthaulax* is not closely related to the Recent American species.

Further, a number of fossil strombid species are known from South America, dating as far back as the Eocene. These have been allocated to various (sub-)genera, like *Oostrombus* Sacco, 1893 (type species *Strombus problematicus* Michelotti, 1861) but are probably not closely related to the Recent species and may belong to another clade which has become extinct.

SYSTEMATICS

Family Strombidae Rafinesque, 1815

Persististrombus Kronenberg and Lee *gen. nov.*

Type species: *Strombus granulatus* Swainson, 1822 Pliocene to Recent

Description: Shell of moderate size for family, fusiform, shoulder knobs distinct on body whorl, slightly expanded outer lip with sharp, unglazed rim and no extensions, regularly divided callus on columella, anterior canal short, posterior canal or groove absent or obsolete. Protoconch elongate and conical with four to five smooth whorls. Adaxial side of outer lip smooth, plicate, or granulate.

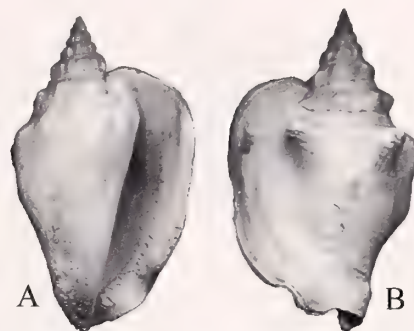


Figure 1. *Persististrombus aldrichi* (Dall, 1890). U.S.A., Florida, Calhoun Co. Chipola River just above Farley Creek Chipola Formation, Early Miocene. Leg. C. Hertweck, collection H. G. Lee. Actual size 47.9 mm. A. Apertural view, B. Dorsal view. Photos H. G. Lee.

Derivation: Derived from the Latin *persistens* (persistent) combined with *Strombus*, as the general shell morphology of species assigned to this genus has remained almost unchanged from the Early Oligocene (Lozouet & Maestrati, 1986) to Recent. The late Eocene record by Lozouet and Maestrati (1986) for *S. radix* may be erroneous (personal communication Lozouet to GCK, January 2007).

Other species assigned to *Persististrombus* *gen. nov.* are: *Strombus aldrichi* Dall, 1890 from the early Miocene of the Chipola Beds, Florida, U.S.A. (Figure 1); *S. baltrae* García-Talavera, 1993 from the Pliocene of Isla Baltra, Islas Galápagos; *S. barrigoniensis* Jung & Heitz, 2001 from the Cubagua Formation, early Pliocene of Venezuela; *S. bonellii* Brongniart, 1823 from the Early Miocene of France (Figures 2, 3) [this may be a junior synonym of *S. nodosus* Borson, 1820, *cf.* Sacco (1893:4)]; *S. insulanus* Jung & Heitz, 2001 from the Escudo de Veraguas Formation, middle Pliocene of Panama; *S. mardieae* Petuch, 2004 from the early Miocene of the Chipola beds, Florida, U.S.A.; *S. obliteratus* Hanna, 1926 from the Pliocene of Imperial County, California, U.S.A.; *S. radix* Brongniart, 1823 from the Early Oligocene of Europe (Figure 4); *S. toroensis* Jung & Heitz, 2001 from the Cayo Agua Formation, early Pliocene of Panama; a radiation of the Middle Miocene of Europe (Harzhauser & Kronenberg in prep.) and a number of species reported by Jung & Heitz (2001) which are identified by means of open nomenclature or by letters. Powell (1988:17) also listed a – possibly new – species which he allocated to *Strombus* (*Lentigo*), but specimens of it haven't been examined by us. This species is not unlikely a *Persististrombus* as well. We agree with Jung & Heitz (2001:28) that *S. granulatus cortezianus* Durham, 1962 [new name for *S. granulatus acutus* Durham, 1950 *non* G. Perry, 1811] is a synonym of *S. granulatus*. For an overview of species allocated to



Figure 2. *Persististrombus bonellii* (Brongniart, 1823). France, Dept. Gironde, Le Peloua. Burdigalian, Early Miocene. Leg. B. Landau, collection B. Landau. Actual size 86.8 mm. A. Apertural view, B. Apical view, C. Dorsal view. Photos B. Landau.

Persististrombus gen. nov. through time and space, see Table 1 and Figure 5.

Although *Persististrombus* gen. nov. has a number of characters in common with *Lentigo* Jousseaume, 1886 (TS by monotypy: *Strombus lentiginosus* Linnaeus, 1758), there are conspicuous differences: in *Lentigo* the adapical part of the outer lip has two notches, resulting in two lobes, of which the most adaxial one is attached to the spire of the shell; species assigned to *Lentigo* have



Figure 3. *Persististrombus bonellii* (Brongniart, 1823). France, Dept. Gironde, Le Peloua. Burdigalian, Early Miocene. Leg. B. Landau, collection B. Landau. Actual size 83.0 mm. A. Apertural view, B. Dorsal view. Photos B. Landau.



Figure 4. *Persististrombus radix* (Brongniart, 1823). France, dept. Landes, Espibos, Gaas. Chattian, late Oligocene. Leg. B. Landau, collection B. Landau. Actual size 64.0 mm. A. Apertural view, B. Apical view, C. Dorsal view. Photos B. Landau.

a more distinct posterior canal, a number of small triangular extensions at the abapical side of the outer lip on the flange between the stromboid notch and the anterior canal, very often rather worn in *L. lentiginosus*, and a columellar callus which does not reach the base of the columella, but is thickened at its abapical part, but not forming a distinct pad as in some species of *Euprotomus*. Species assigned to *Persististrombus* gen. nov. also have a relatively higher spire than do species of *Lentigo*, but within *Persististrombus* gen. nov. species with a low spire do occur (Harzhauser & Kronenberg, in prep.). *Lentigo* is here considered to be restricted to the Indo-Pacific; see also Kronenberg & Vermeij (2002). *Persististrombus* gen. nov. has many characters in common with *Strombus* Linnaeus, 1758 (type species by SD Montfort, 1810: *Strombus pugilis* Linnaeus, 1758), especially the spire. Differences between *Persististrombus* gen. nov. and *Strombus* are more difficult to quantify, and are more qualitative. In *Strombus* the tips of the shoulder knobs are pointed whereas in *Persististrombus* gen. nov. these tips are usually rounded. But the population of *P. granulatus* from the Islas Galápagos has the tips of the shoulder knobs, better referred to as spines, pointed. In *Strombus* there is no sculpture in the form of knob-like structures abapical of the row of these shoulder knobs. In *Persististrombus* gen. nov. there usually are one or sometimes two of such rows, but in the middle Miocene of Europe there is at least one species of *Persististrombus* gen. nov. which only has the shoulder knobs present, and again the population of *P. granulatus* from the Islas Galápagos does not have

Table 1
Distribution in time and space of *Persististrombus* gen.nov. species.

Species	Age	Locality
<i>P. radix</i>	Oligocene	Mediterranean region
<i>P. bonellii</i>	early Miocene	Mediterranean region
<i>P. aldrichi</i>	early Miocene	Florida, U.S.A.
<i>P. mardia</i>	early Miocene	Florida, U.S.A.
<i>P. spp. Vienna basin</i>	early middle Miocene	Vienna Basin, Austria
<i>P. cf. insulanus</i>	early middle Miocene	Grenadines
<i>P. sp. C (Jung and Heitz)</i>	middle – late Miocene	Venezuela
<i>P. sp. A (Jung and Heitz)</i>	late Miocene	Venezuela
<i>P. barrigonensis</i>	early Pliocene	Venezuela
<i>P. toroensis</i>	early Pliocene	Panama
<i>P. sp. E (Jung and Heitz)</i>	early Pliocene	Jamaica
<i>P. insulanus</i>	middle Pliocene	Panama
<i>P. obliteratus</i>	Pliocene	California, U.S.A.
<i>P. sp. B (Jung and Heitz)</i>	Pliocene	Panama
<i>P. baltrae</i>	Plio-Pleistocene	Islas Galápagos
<i>P. granulatus</i>	late Pliocene – Recent	Panamic fauna province
<i>P. sp. D (Jung and Heitz)</i>	Pleistocene	Panama

a second or third row of knobs present in all specimens (Kronenberg & Lee, 2005). Fossil species of *Strombus* s.s. may have spiral sculpture (e.g., *Strombus lindae* Petuch, 1991; see Petuch 1994: pl. 21, fig. A) as grooves on the body whorl. But also the “*nicaraguensis*” form of *Strombus pugilis* (see Clench & Abbott, 1941: pl. 6) has this kind of spiral sculpture on (part of) the body whorl. In *P. aldrichi* this sculpture, though less conspicuous, is present, but the abapical part of the

body whorl is never smooth as in *Strombus*. In *Strombus* the outer lip is more widely expanded than in *Persististrombus* gen. nov., and the adapical aspect of the outer lip (wing) is more or less pointed (not very evident in all specimens of *S. alatus*). This outer lip expansion is particularly evident in the apical view: In *Strombus* the labrum arches ventrally from its posterior origin at the suture so as to form a large open sinus with its free margin directed abaxially, whereas that

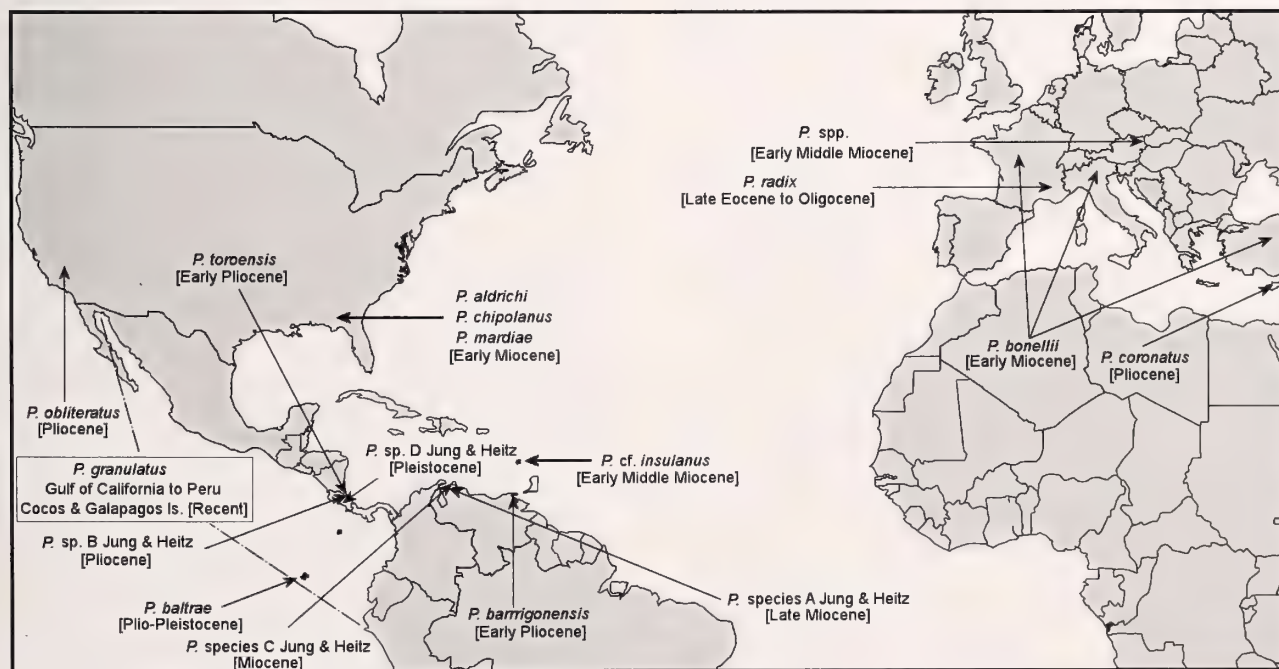


Figure 5. Geographic and Stratigraphic Distribution of *Persististrombus* gen. nov. species.

Table 2

Summary of distribution and characters of *Lentigo*; *Persististrombus* gen. nov.; *Strombus*; and *Lobatus*.

	<i>Lentigo</i>	<i>Persististrombus</i>	<i>Strombus</i>	<i>Lobatus</i>
Zoogeographical province	Indo-Pacific	Parathetys – Caribbean – Panamic	Caribbean – Panamic	? Parathetys – Caribbean – Panamic
Tip of shoulder knobs	rounded	rounded	pointed	rounded
Knobs abapical of shoulder knobs	present	usually present	absent	usually absent
Spiral grooves in adult species	absent	absent	absent or present	present
Outer lip	slightly expanded	slightly expanded	clearly expanded	clearly expanded
Transition lateral part outer lip to adapical part outer lip	rounded	rounded	pointed; not always clear in <i>S. alatus</i>	Variable, from rounded to pointed, but when pointed forming a distinct groove from tip of point into the aperture
Abapical part of outer lip	bilobed	simple	simple	simple
Triangular projections between strombid notch and anterior canal	present	absent	absent	absent
Columellar callus	thickened abapical	not thickened	not thickened	not thickened

aspect of *Persististrombus* shows a narrower sinus which tends to curve adaxially at its free margin. Juveniles of *P. granulatus* (see e.g., Emerson & Old, 1963:8 fig. 7) have a distinct spiral sculpture, a character which they share with *Strombus*. *Strombus* is restricted to America, and it may have been derived from a species of *Persististrombus* gen. nov.

Persististrombus gen. nov. differs from other American species, here assigned to *Lobatus* Iredale, 1921, in rate of expansion of the outer lip and sculpture of the body whorl. Several genus level taxa for these American species are available, viz. *Aliger* Thiele, 1929 (TS *Strombus gallus* Linnaeus, 1758); *Eustrombus* Wenz, 1940 (TS *Strombus gigas* Linnaeus, 1758); *Macrostrombus* Petuch, 1994 (TS *Strombus costatus* Gmelin, 1791); and *Titanostrombus* Petuch, 1994 (TS *Strombus goliath* Schröter, 1805 [not 1905 (Petuch, 1994:261), an apparent *lapsus calami*]). The relationships within these American species are still unclear, and whether these should be regarded as subgenera of *Lobatus* is beyond the scope of the present paper; see table 2.

Persististrombus granulatus occurs from the northern end of the Gulf of California (Sea of Cortez) to Ecuador (Keen, 1971:421). Skoglund (2002:55) added some records to the known distribution, including Isla Gorgona (Colombia) and Islas del Coco (Costa Rica) southward to Zorritos, Perú. Finet (1994) listed Islas Galápagos and provided other references in support.

Given the rather aberrant shape of some of the specimens originating from the Islas Galápagos in comparison to the continental specimens of *P. granulatus*, we believe a process of speciation of the Galápagos population is emerging. This speciation may, however, be frustrated by an infrequent influx of

larvae originating from the continental population. It seems that there is a genetic factor involved in the various insular populations' phenotypy. There may even be significant segregation of genomes among populations of *P. granulatus* (s.l.) by island or group of islands in the Galápagos. The islands may be the metaphorical battlefield for the (genetic) independence of the earlier immigrant waifs [as in the Isla Santa Fé morphs, see illustrations in Kronenberg & Lee (2004)]. However, at present we see no constant difference in characters of the shells to make a clear conchological separation among populations. We are aware that there is no proof for this hypothesis, and therefore this is highly speculative at present. However, this hypothesis can probably be tested by molecular analysis.

A NOTE ON *LOBATUS* IREDALE, 1921

Jung and Heitz (2001:48–50, fig. 26) described *Strombus fetus* from the Escudo de Veraguas Formation (late Pliocene) of Panama and assigned this species to the subgenus *Lentigo*. They based their description on only one specimen and stated that this species is not related to any of the species they studied, stating that *S. fetus* resembles *S. raninus* Gmelin, 1791 only superficially. They mentioned only one difference, viz. the size of the knobs on the shoulder of the body whorl. Indeed, most specimens of the Recent *S. raninus* have two large, spine-like knobs on the shoulder of the body whorl, which character is expressed in the nomen *S. bituberculatus* Lamarck, 1822, a synonym. Yet this is not always the case. In the private collection of the first author there are two specimens, viz. one from Aruba, Paardenbaai, inside reef in seaweed field, leg. Jan Berkhout, 1967 (GCK 5419); one from Aruba, Secoe di

Palma, *leg.* Jan Berkhout, 1968 (GCK 5423) in which the two last knobs on the shoulder of the body whorl are only slightly enlarged and one specimen from Panama, Isla Bastimentos, Bocas del Toro, found dead in surf zone, *leg.* Monika Forner, 30 November 1997 (GCK 5858) in which the development of the shoulder knobs is not different from *S. fetus* as illustrated by Jung & Heitz. After studying the description and illustrations, we regard *Strombus fetus* as a synonym of *S. raninus*, which may also be true for *S. praeranus* Kronenberg & Dekker, 2000 [new name for *Strombus wilsonorum* Petuch, 1994 *non* Abbott, 1967] and *Strombus magolecciai* Macsotay & Villaroel, 2001.

Petuch (1994) named a number of fossil Caribbean strombid taxa, both at the genus and species level. For *Strombus raninus*, Petuch used the subgenus name *Lobatus* Iredale, 1921. Jung and Heitz (2001:40) criticized the use of the name *Lobatus* by Petuch because the introduction of *Lobatus* was an historical accident, referring to Abbott (1960:53). However, the introduction of *Lobatus* by Iredale (1921:208) meets the requirements of the ICZN (Article 12.2.5), and therefore the name *Lobatus* Iredale, 1921 (TS *Strombus bituberculatus* by monotypy) is available.

POSSIBLE PHYLOGENIES OF RECENT AMERICAN STROMBIDS

Kronenberg & Vermeij (2002:53) argued that the Recent Western Atlantic and Panamic strombids (including the West African *Strombus latus* Gmelin, 1791, and excluding the Indo-Pacific *Gibberulus gibbosus* (Röding, 1798) which was reported by Mienis (1978) from the Islas Galápagos [as *Strombus* (*Gibberulus*) *gibberulus gibbosus*]), are monophyletic. This may be true because we have not been able to trace any fossil evidence of any *Strombus* (s.l.) in the Western Atlantic fossil record before *Persististrombus* gen.nov. made its appearance there.

Within this possible clade a number of groups (based on overall shell characters, and for which genus-level names are available; see above) can be discerned, *viz.*: *S. costatus*; *S. gigas*; *S. raninus* + *S. peruvianus* + *S. gallus*; *S. goliath* + *S. galeatus*. It should be noted here that in the analysis of stromboidean genus-level taxa, based principally on anatomical characters, Simone (2004) puts *Strombus raninus* (allocated to *Tricornis* by Simone) apart from the other American strombid species, i.e., branching off before *Lambis*, while all other American strombid species (as far as examined by Simone) branch off after *Lambis*.

Some possible scenarios for a phylogeny of the American species can be taken into consideration. With no pretense to an exhaustive presentation, we mention a few such, which can be tested using molecular data.

Scenario 1)

All recent American species are descendants of a species which is also ancestral to the recent *P. granulatus*. This may have happened in one single wave (that is that one species of *Persististrombus* is ancestral to all western Atlantic and Panamic Recent species) or in two (or more) waves in which one of these waves ended up in *S. pugilis*, *S. alatus* and *S. gracilior*; the other(s) resulted in all other species. Based on the molecular data as presented by Latiolais *et al.* (2006) this scenario of two waves seems most likely.

Scenario 2)

Sacco (1893:12) postulated that the late Miocene to late Pliocene *Strombus coronatus* De France, 1827 (from the Tortonian through Piacenzian of Europe) is ancestral to both the Recent West African *Strombus latus* (as *Strombus bubonius* Lamarck, 1822) and the Recent *Strombus costatus* (as *Strombus accipitrinus* Lamarck, 1822). All three of these species are extremely variable (see for *Strombus* (s.l.) *coronatus* e.g., Sacco, 1893, pl. 1, for *Strombus* (s.l.) *latus* DeTurck *et al.* pls 102, 103 and for *Strombus* (s.l.) *costatus* DeTurck *et al.* pls 43, 44), and a large number of names are available, especially for *S. coronatus*; see Sacco (1893).

Beneventi & Piccoli (1969), based on a number of fossil species, elaborated on this scenario and concluded that many Recent species descend from a lineage started by *Strombus fortisi* Brongniart, 1823 through *S. radix* and *S.* (s.l.) *coronatus*, to Recent Western Atlantic and Panamic province species, but also to Recent Indo-Pacific species assigned to *Euprotomus* and *Lentigo*. [The evolution of *Persististrombus* in Europe, except for *P. radix* and *P. bonellii* will be discussed elsewhere (Harzhauser & Kronenberg, in prep.)]. In their tree (Beneventi & Piccolo, 1969:17) *Persististrombus granulatus* also descended from *Strombus coronatus*, contrary to the results as shown by Jung & Heitz (2001) and our view. Also, the loss of the extremely dilated outer lip, as in *Dilatilabrum*, in *Persististrombus radix* and the subsequently regaining such a wing as present in many of the western Atlantic and Panamic fauna province species, seems unlikely.

However, a derivation of some Indo-Pacific species from a strombus radix-like species is not that unlikely. There are some morphological characters which link *bernielandawi* Harzhauser, 2007, from the Oligocene late Chattian Warak formation, Gebel Madrasah, Oman, *S. gijskronenbergi* Harzhauser, 2007 from the Miocene Aquitanian Gubbarah formation, Gebel Madrasah, Oman, *S. quilonensis* Dey, 1961 from the ?late Miocene of southern India and *Strombus pre-occupatus* Finlay, 1927 from the early to late Miocene of Java and Borneo (Indonesia) although the knobs are more strongly developed and much more spine-like,

reminiscent of *Strombus coronatus* and *Strombus latus*, and to some degree resembling *Persististrombus*.

Strombus preoccupatus was first assigned to *Lentigo* (as a subgenus) by Abbott (1960:123) but later (1965:402) transferred to *Dolomena* Wenz, 1940 (also as a subgenus). [*Dolomena* Iredale, 1931:212 is a *nomen nudum*, see Kronenberg & Dharma, 2005]. *Strombus sedanensis* Martin, 1899 of the early Miocene of Indonesia and Pakistan was assigned to *Dolomena* (as a subgenus) by Abbott (1960:102). This was followed by Raven (2002:13, pl. 5 fig. 26a, 26b) with *Dolomena* as a genus. In general shape *Strombus sedanensis* also reminds one of certain forms of *S. coronatus*, *S. latus*, and, to a lesser extent, as the outer lip of that species is clearly more dilated, *S. costatus*. Without providing an allocation for both these species, we reject the assignment of *S. sedanensis* to *Lentigo* (see remarks under description of *Persististrombus* gen. nov.) or *Dolomena*, because the structure of the outer lip clearly differs from species of that latter genus. Other species from the Miocene of Indonesia, such as *S. inflatus* Martin, 1879, *S. herklotsi* Martin, 1880, *S. tuberosus* Martin, 1883, *S. tjilonganensis* Martin 1899, as well as *S. mekranicus* Vredenburg, 1928 from the Miocene of Pakistan (all allocated to *Tricornis* by Abbott, 1960:61–62) should be critically re-examined in terms of their generic position and possible relation to the Recent and fossil Indo-Pacific species mentioned above. This task is beyond the scope of the present report.

Scenario 3)

The genus *Dilatilabrum* Cossmann, 1904 [TS *Strombus fortisi* Brongniart, 1823 from the Lutetian (middle Eocene) of Italy] may have been ancestral to (some of) the broad winged species. Species of *Dilatilabrum* are characterized by a widely-dilated outer lip (wing) and a large, narrow keel on the shoulder of the dorsal side of the body whorl. Based on the general shape and the presence of a keel-like ridge on the dorsum, both *S. dominator* Pilsbry & Johnson, 1917 from the Miocene of Santo Domingo, Dominican Republic and *S. dominator delabechei* Rutsch, 1931, known from the Pliocene Bowden Formation of Jamaica, could be assigned to *Dilatilabrum*, thus linking the Eocene *S. fortisi* to the Recent broad winged species. But *S. dominator* s.s. and *S. dominator delabechei* have a shallow strombid notch and a more or less clearly developed spiral sculpture on the latter part of the last whorl, both absent in *D. fortisi*. The large *D. roegli* (Harzhauser, 2001) [as *Strombus (Dilatilabrum) roegli*] from the Oligocene of Greece and Iran does have a strombid notch, but does not have the spiral sculpture present in *S. dominator* s.l.. Based on the consensus tree as presented by Latiolais *et al.* (2006:440) we do not think that the genus *Dilatilabrum* is closely related to the

modern fauna, and disappeared during the extinction wave at the end of the Eocene leaving only *D. roegli* to persist into the Oligocene, when it perished.

Savazzi (*vide* Harzhauser, 2001:58) suggests that the strombid notch evolved twice. Given the presence of the strombid notch in some other grades or clades of Stromboidea (Pugnelliidae; see remark by Kronenberg & Burger, 2002:43) and *Rimella*-like species, *Ectinochilus*, *Varicospira* and other genera (Clark & Palmer, 1923; Burger & Kronenberg, 2006), we suggest that this character may have arisen even more than twice.

Simone (2005: 248) used the absence of a strombid notch in Recent *Lobatus goliath* as a reversion in his listing of characters he used in his analysis. This strombid notch, however, is present in some specimens of *L. goliath*, and the absence of the notch in certain specimens is here considered not to be a reversion as argued by Simone (2005) but part of the intraspecific variation of this species.

The position of *Strombiconus* Marks, 1951 (TS *Strombiconus ecuadorensis* Marks, 1951, which is the only species ever assigned to this genus) from the Early Miocene of Ecuador is enigmatic. The two known specimens on which both the description of the species and the genus were based are juveniles with worn apices (Marks, 1951:141–142, pl. 9 figs 10–11), and the systematic position of this genus and species, although probably strombid, cannot be determined. The same is true for the more recently described *Austrombus* Nielsen, 2005 (TS *Conus medinae* Philippi, 1887) from the Miocene of Chile, as already acknowledged by Nielsen (2005:1122).

The overriding problem of convergence in the Strombidae impedes a morphological analysis of evolutionary relationships. An example is the resemblance between *Lobatus gallus* and *Tricornis tricornis* and the above-mentioned close resemblance of *Dilatilabrum* with some of the fossil and Recent Caribbean and Panamic species. What appears to emerge is a mosaic pattern of characters that appear, disappear and reappear between lineages, but also within one single lineage, see also Landau *et al.* (in prep.) We agree with Petuch (1994:258) that none of the American species should be assigned to *Tricornis* Jousseaume, 1886, which only superficially resembles certain of these American species.

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Drill Holes in Bathymodiolin Mussels from a Miocene Whale-fall Community in Hokkaido, Japan

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Abstract. Three specimens of *Adipicola chikubetsuensis* (Amano) with drill holes ranging from 0.9 mm to 1.2 mm in width were found in a Miocene whale-fall community in northern Hokkaido, Japan. This is the first record of drilled chemosymbiotic mussels (bathymodiolins) and of drilling predation at whale-falls. With two percent of the recovered mussels being drilled, the drilling intensity at this whale-fall site is low compared to that among mytilids and other heterotrophic bivalves in shallow water environments. This low drilling intensity may be caused by the low tolerance of naticids for sulfide. We propose that the delayed onset of naticid predation at whale falls in the Miocene relates to the changing mechanism of sulfide production at whale-falls at the transition from the Oligocene to the Miocene.

INTRODUCTION

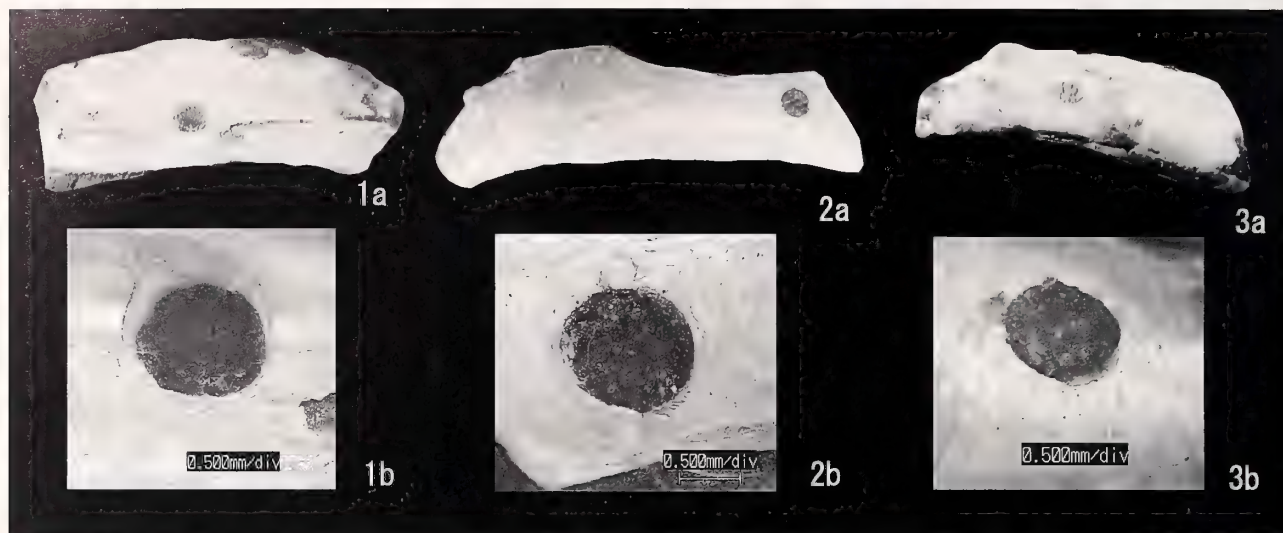
Chemosymbiotic macrofauna such as tube worms, clams, mussels, snails, and crustaceans has been found in deep-sea reducing microenvironments around hydrothermal vents, cold seeps, whale-falls, and sunken wood (e.g., Van Dover, 2000). Predation is known to structure the faunal composition of these communities (Micheli et al., 2002) and has also been suggested as a major factor in the confinement of these communities to water depth below 350 m (Sahling et al., 2003). Most higher taxa of the modern vent and seep macrofauna appeared in the late Mesozoic (Little & Vrijenhoek, 2003; Kiel & Little, 2006), concurrent with the Mesozoic Marine Revolution (Vermeij, 1977, 1987). Thus predation may also have played an important role in the evolution of invertebrate communities in these extreme environments.

Unfortunately, direct evidence for predation, such as drill holes in molluscan shells from fossil chemosynthetic environments, is still sparse. Most records are from Eocene to Miocene cold seeps in Japan, and a few additional examples are known from the Oligocene of Washington State, USA. Amano (2003a) described drill holes in the vesicomyid *Calyptogena pacifica* Dall and in the thyasirid *Conchocele bisecta* (Conrad) from the upper Miocene Morai Formation in Hokkaido that were presumably made by the co-occurring naticids *Euspira pallida* (Broderip & Sowerby) and *Cryptonatica* sp. *Calyptogena pacifica* with an unsuccessful drill hole

was described from the upper Miocene Nodani Formation in central Honshu by Amano & Kanno (2005). Amano & Jenkins (2007) noticed that a specimen of *Adulomya chitanii* Kanehara illustrated by Kamada (1962) from the lower Miocene Taira Formation in the Joban coal-field was drilled successfully, and the vesicomyid *Hubertschenkia ezoensis* (Yokoyama) and *Conchocele bisecta* with drill holes presumably made by *Euspira?* sp. were collected from the upper Eocene Poronai Formation in Hokkaido (Amano & Jenkins, 2007).

On the eastern side of the Pacific Ocean, from cold-seep carbonates in the Oligocene part of the Lincoln Creek Formation in Washington State, Kiel (2006) reported a drill hole in a specimen of the nuculanid bivalve *Nuculana?* cf. *grasslei* Allen, and one specimen of *Provanna antiqua* Squires with a healed injury probably caused by a crab. In addition, we recently found a drilled vesicomyid in cold-seep carbonates in the same sediments (Amano & Kiel, 2007). The oldest evidence for predatory animals at seeps are crustacean fragments and coprolites from Late Jurassic (Oxfordian) methane seep deposits near Beauvoisin in southern France (Senowbari-Daryan et al., 2007), but there are no traces of shell peeling or crushing in the mollusk shells from that site (SK, personal observation).

In this paper we present the first direct evidence for predation at a fossil whale-fall site. Newly collected material from the Miocene 'Shosanbetsu' whale-fall site



Figures 1–3. Drill holes in *Adipicola chikubetsuensis* (Amano) from the middle Miocene Chikubetsu Formation in Hokkaido, Japan. The upper figures show the complete specimens, the lower figures are close-ups on the drill holes. Fig. 1a, b, JUE no. 15821-1; Figs. 2a, b, JUE no. 15850; Figs. 3a, b, JUE no. 15821-2.

(cf. Amano & Little, 2005) yielded three specimens of the bathymodiolin *Adipicola chikubetsuensis* (Amano) with drill holes. These specimens are described and their significance is discussed.

OCCURRENCE

The Shosanbetsu whale-fall community occurs in concretions within siltstones of the uppermost part of the lower middle Miocene Chikubetsu Formation, at a road-cut on the northern side of the Setakinai River; about 5.5 km upstream from Shosanbetsu Village in northwestern Hokkaido (see Figure 1 of Amano & Little, 2005). *Adipicola chikubetsuensis* and the gastropod *Provanna* sp. dominate the community, minor elements are *Adulomya hokkaidoensis* Amano & Kiel, *Solemya* sp., the buccinid *Trominina* sp., and a poorly preserved naticid. Based on foraminifers, this part of the Chikubetsu Formation was probably deposited in water deeper than the middle bathyal zone (Maiya et al., 1982). From a total of 121 specimens of *Adipicola chikubetsuensis*, the shells of three specimens had drill holes. Almost all of the specimens are articulated and occurred in dense clusters without any apparent orientation directly attached or a few millimeters away from the whale bones. All of the studied drilled shells are housed at the Joetsu University of Education (JUE).

DRILL HOLE DETAILS

Among 121 specimens of *Adipicola chikubetsuensis* only three specimens (2%, which equals a drilling intensity of 0.02) have drill holes. The most common mode of preservation of these shells is that the outermost

(calcitic?) layer is detached from the nacreous inner layer, and both sides adhere to their respective side of the concretion. In two cases the drill holes are preserved on the outer side of the inner layer of a right and a left valve (Figure 1a, b, 3a, b), in one case it is preserved on the inner side of the outer layer of a left valve (Figure 2a, b). The drill holes are small with a diameter ranging from 0.9 to 1.2 mm, have a circular or elliptical outline (Table 1), and, considering the protruding shape shown on Figure 1b, they are parabolic in cross section. All three holes occur at the central portion of the shell, where the ventral margin is most concave. We have not seen drill holes in any of the other species that occur at the Shosanbetsu whale-fall site.

DISCUSSION

Generally, parabolic drill holes are attributed to naticids, and cylindrical drill holes to muricids (e.g., Aitken and Risk, 1981). The holes in *Adipicola chikubetsuensis* at the Shosanbetsu whale-fall site are parabolic and are drilled in the central portion of the shells. This is a common position for naticid drill holes in Recent mytilids. For example, Griffiths (1981) reported that *Tectonatica tecta* (Anton) drilled the central part of the shell of the South African *Choromytilus meridionalis* (Krauss), and in the western Atlantic *Euspira heros* (Say) has been observed to drill *Mytilus edulis* Linnaeus at this position (G. Dietl, personal communication, 2007). Considering the shape and position of drill holes and that four small naticids were found at the Shosanbetsu whale fall site while muricids appear to be absent (Amano & Little, 2005;

Table 1
Measurements of the holes in *Adipicola*
chikubetsuensis (Amano).

Specimens	Shell length (mm)	Diameter of hole (mm)
JUE no. 15821-1	12.2+	1.2
JUE no. 15821-2	11.9+	0.9
JUE no. 15850	16.9+	1.1

present study), it seems straightforward to assume that the drill holes reported here were made by naticids.

Reports of naticid predation of mussels in shallow water are rare (Edwards, 1975; Griffiths, 1981), whereas predation by muricids occurs quite frequently (Wright & Francis, 1984; Vermeij et al., 1989; Harper & Skelton, 1993; Gordillo, 2001). This is not very surprising considering that mussels are usually byssally attached to some sort of hard substrate, a habitat frequently visited by muricids but not by naticids, which are soft-bottom dwellers (Taylor et al., 1980). A clue to how and why naticids may be able to attack mytilids at whale falls was provided by Okutani et al. (2003, p. 62), who reported *Adipicola pacifica* specimens from experimentally submerged whale bones in 219 to 254 m depth offshore Cape Nomamisaki (Kyushu, Japan) that were actively moving around using their foot, and *A. crypta* specimens from the same bones that were living very close to the sediment-water interface. Such specimens are potentially available for sediment-dwelling naticids like *Tanea magnifluctulata* (Kuroda), which was reported from near that whale-fall community (Okutani et al., 2006). It is likely that also the Miocene *Adipicola chikubetsuensis* at the Shosanbetsu whale-fall site lived very close to the sediment and would thus be accessible for the co-occurring naticids.

However, Gordillo (1994, 1998) showed that also the trophonine muricid *Trophon geversianus* Pallas produces parabolic holes, and Recent trophonines are thought to drill *Calypptogena gallardoi* Sellanes & Krylova and *Thyasira methanophila* Oliver & Sellanes at methane seeps off Concepción in Chile (Houart & Sellanes, 2006). Thus, the possibility remains that undetected trophonines are responsible for the drill holes in *Adipicola chikubetsuensis* at the Shosanbetsu whale-fall site.

Interestingly, drill holes have neither been found in the Eocene and Oligocene whale-fall communities in Washington State, USA, nor in the wood-falls in the same sediments, although naticids and muricids were present (Goedert et al., 1995; Kiel & Goedert, 2006a, b, and unpublished data). This led Kiel & Goedert

(2006b) to suggest that in the case of the Eocene and Oligocene wood-falls the 'naticid'-like shells may in fact belong to the herbivore gastropod family Ampullinidae (= Ampullospiridae of some authors) which builds shells that are convergent in shape to those of naticids (Bandel, 1999; Kase & Ishikawa, 2003). Kiel & Goedert (2006a) proposed that whale-fall communities in the Eocene and Oligocene resembled wood-fall communities in that the sulfide used by chemosymbiotic bivalves was derived from a cover of organic material around the whale skeleton, analogous to the cover of shipworm fecal pellets around wood falls. At modern-type whale falls from the Miocene onwards sulfide is released from the bones as a result of anaerobic breakdown of bone lipids (Smith & Baco, 2003).

This ecologic difference between the Eocene and Oligocene whale falls on the one hand, and the Miocene to modern ones on the other, may also affect naticid predation. Naticids are very rare at seeps (Warén & Bouchet, 2001) and may have a low tolerance for sulfide. Thus they might have disliked the carpet of decaying organic material around the early whale falls (and wood falls, too), whereas at the Miocene to modern whale falls the sulfide is very localized at the bones and may not form a barrier for the naticids. However, this interpretation is based on very few data and needs to be tested when more information on modern and fossil whale-fall communities and their ecology becomes available. Although naticids are known from modern whale-falls (Okutani et al., 2006) there is no direct evidence yet for their drilling activities.

The drilling intensity among the bathymodiolins at the Shosanbetsu whale-fall is about 0.02. Except for two cases (0.20 in *Calypptogena pacifica* from the Morai Formation and 0.27 in the Recent *Thyasira methanophila*), drilling intensities in deep-sea chemosynthetic environments do not exceed 0.1 (Table 2). Shallow-water heterotrophic bivalves usually show higher intensities. For example, naticid predation on *Glycymeris* in the Neogene of Japan and the US east coast usually has intensities above 0.1 and occasionally reaches more than 0.6 (Thomas, 1976; Amano, 2003b, 2006). A similar range was recognized in North American bivalve assemblages from the Cretaceous through Recent (e.g., Kelley & Hansen, 2003). Based on the few data presently available, drilling intensities in chemosynthetic environments appear low compared to shallow marine environments. Although drilling activities at cold seeps start in the late Eocene, the drilling intensities show no increase or other tendencies through time. The most likely explanations for these low drilling intensities at chemosynthetic environments are the reducing conditions at these sites and symbiont-bearing species may be protected from predation by metabolites produced by the chemoautotrophic endo-

Table 2

Drilling intensities in fossil and Recent chemosynthetic communities. DI = Drilling intensity.

Age	Site	Species	DI	References
Recent	Cold Seep	<i>Thyasira methanophila</i>	0.27	Houart & Sellanes (2006)
		<i>Calypptogena gallardoi</i>	0.01	Houart & Sellanes (2006)
Late Miocene	Cold seep	<i>Conchocele bisecta</i>	0.09	Amano (2003)
		<i>Calypptogena pacifica</i>	0.20	Amano (2003)
Middle Miocene	Whale fall	<i>Adipicola chikubetsuensis</i>	0.02	Present study
Late Eocene	Cold seep	<i>Conchocele bisecta</i>	0.09	Amano & Jenkins (2007)
		<i>Hubertschekia ezoensis</i>	0.06	Amano & Jenkins (2007)

symbionts that deter predators from feeding on them (Kicklighter et al., 2004).

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Fossil Vesicomyid Bivalves from the North Pacific Region

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Abstract. A review of the fossil record of vesicomyid bivalves from the North Pacific region (Hokkaido, Japan; Alaska and Washington, USA) allows the clarification of the status of several species based on new data and observations, and four new species are recognized. Detailed examination of the hinge of *Hubertschenckia ezoensis* shows that *Hubertschenckia* is a valid monotypic genus closely related to *Archivesica* and *Calyptogena*. Specimens of ‘*Calyptogena*’ *chinookensis* from its late Eocene type locality at Bear River have a hinge structure that clearly places this species in *Adulomya*; silicified ‘*C.*’ *chinookensis* specimens described earlier from the late Oligocene have a very different hinge structure and are assigned to the new species *Archivesica knapptonensis*. The hinge dentition of all three Cretaceous vesicomyids proposed so far is unknown and their validity is doubtful. With *Hubertschenckia ezoensis*, *Adulomya chinookensis*, and *Archivesica* cf. *tshudi*, three genera of large vesicomyids appear more or less simultaneously at methane seeps in the late Eocene. Of Oligocene age are the new species *Archivesica georgemoorei* from Alaska, which is shorter and more oval than other known *Archivesica* species, and a possible *Pliocardia?* sp. from cold seeps in Washington. From the early Miocene of Washington *Isorropodon frankfortensis* is described and represents the first certain record of this genus from outside the Atlantic realm. The new middle Miocene *Adulomya hokkaidoensis* is so far only known from a whale-fall community in Hokkaido and may have been endemic to this type of habitat. The timing of the occurrences of these taxa shows no correlation to the evolution of whales in this area, shedding further doubt on the ‘whale stepping-stone’ hypothesis for the origin of vesicomyids.

INTRODUCTION

Fossil vesicomyid bivalves in the North Pacific region, especially in Japan, have been described for more than a century (Yokoyama, 1890; Majima et al., 2005; Amano & Kanno, 2005). However, vesicomyids received little scientific attention until the discovery of the ‘Giant White Clam’ *Calyptogena magnifica* at hydrothermal vents on the Galapagos Ridge in the late 1970s (Boss & Turner, 1980). Since then they have been found in many chemosynthesis-based ecosystems at hydrothermal vents, hydrocarbon seeps, and whale carcasses throughout the world’s oceans (Van Dover, 2000; Van Dover et al., 2002; Kojima, 2004). These discoveries led paleontologists to take a new look at vesicomyid occurrences, and many of these sites have since been identified as fossil hydrocarbon-seep deposits.

The occurrence of vesicomyids at decaying whale carcasses in the deep-sea (whale-falls) led to the formulation of the ‘stepping stone’ hypothesis. This hypothesis suggested that whale-falls provide dispersal stepping stones for vent and seep taxa, and that therefore the rise of whales in the Eocene suddenly (geologically speaking) extended the dispersal capabilities of vent and seep taxa, resulting in a significant radiation among these animals (Baco et al., 1999; Smith

& Baco, 2003). This hypothesis was based on the rough correlation between the evolutionary age of vesicomyids estimated from molecular clocks and the first appearance of whales in the Eocene (Baco et al., 1999; Smith & Baco, 2003). Squires et al. (1991) and Goedert et al. (1995) however, had already pointed out that in the North Pacific, seep taxa such as vesicomyid bivalves were already very widely distributed before the earliest known appearance (latest Eocene) of whales in the region. The stepping-stone hypothesis was challenged by Little & Vrijenhoek (2003) who called attention to the discrepancy between the molecular age estimates for vesicomyids [21.5–43.8 Ma according to Peek et al. (1997)] and the oldest fossil vesicomyids from the Early Cretaceous (upper Albian, 106 Ma) in northern Japan (cf. Kanie et al., 1993; Kanie & Sakai, 1997). It was also challenged by Kiel & Goedert (2006) who showed that vesicomyids and other taxa characteristic of modern whale-falls were absent from Eocene and Oligocene whale-falls and only appeared in Miocene examples.

However, a thorough analysis of the fossil history of the Vesicomyidae and its potential correlation with the radiation of whales has so far been hampered by the inconsistent use of generic names and concepts within



Figures 1–4. Locality maps of fossil specimens. Figure 1. Map showing the general location of the fossil sites described herein. Figure 2. Hokkaido, Japan, asterisks indicate the two fossil sites. Figure 3. Kodiak Island, Alaska, asterisk indicates the fossil locality on nearby Sitkalidak Island. Figure 4. Localities in western Washington State, USA, A=Humptulips River sites, B=Canyon River site, C=Satsop River site (LACMIP loc. 17747), D=Bear River site (LACMIP loc. 5802), E=Knappton (LACMIP loc. 5843), F=Frankfort (USGS loc. M2790).

this family (see Krylova & Sahling, 2006 for a review), which partly results from incomplete knowledge of several of the type species. Important progress was made recently by Cosel & Salas (2001) who revised the genera *Vesicomya*, *Waisiuconcha*, *Isorropodon*, and *Callogonia*, by Krylova & Sahling (2006) who redefined *Calyptogena* and revised its Recent species, and by Kiel (2007) who clarified the status of *Pleurophopsis*.

The aim of this paper is to revise some of the fossil vesicomys from the North Pacific region (Figure 1) based on newly collected material. We describe four new species from Japan, Alaska, and Washington, and provide revised generic diagnoses for *Adulomya* Kuroda, 1931, *Archivesica* Dall, 1908, and *Hubertschenckia* Takeda, 1953. Finally, we discuss the evolutionary implications of our findings.

MATERIAL, STRATIGRAPHY, AND OCCURRENCES

All Japanese specimens described here are housed in the Joetsu University of Education (JUE). Material from Washington State will be housed in the Smithsonian Natural History Museum (USNM) and the Natural History Museum of Los Angeles County (LACMIP), the specimens from Alaska will be housed in the Museum of Paleontology, University of California, Berkeley (UCMP). Locality numbers of the United States Geological Survey (USGS) and the

California State University, Northridge (CSUN) are also used herein.

Japan, Hokkaido

Poronai Formation: The Poronai Formation is a 1100 m-thick sequence of deep-water mud- and siltstone of late Eocene age, cropping out in central Hokkaido (Kaiho, 1983, 1984). Seventeen specimens of *Hubertschenckia ezoensis* were collected from a cold-seep deposit at a high cliff along the Ikushunbetsu River, 200 m to the west of Yayoi Town in Mikasa City (Figure 2; see Amano & Jenkins, 2007 for more details). Here, a calcareous concretion approximately 2 m in diameter occurs in dark gray mudstone of the Poronai Formation (B Zone of Teshima, 1955). The *Hubertschenckia* specimens occur mostly within this concretion but also directly adjacent to it. Almost all specimens are articulated, but also a few disarticulated valves were collected. The Yayoi fauna in the surrounding mudstone consists of the protobranch bivalves *Acila* (*Truncacila*) *picturata* (Yokoyama), *Malletia poronaica* (Yokoyama), *Portlandia* (*Portlandella*) *watasei* (Kanehara), the thyasirid bivalve *Conchocele bisecta* (Conrad), the carditid bivalve *Cyclocardia tokudai* (Takeda) and the caenogastropod *Orectospira wadana* (Yokoyama). The faunal composition of the molluscan assemblage is similar to the lower sublittoral to upper bathyal *Malletia poronaica*-

Cyclocardia tokudai assemblage of Suzuki (2000) from the lower part of the Poronai Formation. In addition, Kaiho (1984) used benthic foraminifers to infer a maximum depth of 350 m for deposition of the Poronai Formation.

Chikubetsu Formation: The Chikubetsu Formation is of middle Miocene age and subdivided into the lower sandstones (210 m) and the upper siltstones (230 m) (Noda, 1992). When Amano & Little (2005) recorded a Miocene whale-fall community from the uppermost part of the Chikubetsu Formation, they illustrated two specimens and the hinge of a left valve of *Calyptogena* sp. These were collected from a large roadside cliff along the Setakina River, 5.5 km upstream from Shosanbetsu Village in northern Hokkaido (Figure 2; see Amano & Little, 2005 for more details). Subsequently, one right valve with a distinct pallial line and a specimen with the hinge of the right valve preserved were collected from the same locality. All specimens occurred in a bone-bearing concretion in siltstone. As inferred by Amano & Little (2005), this community might have lived below the middle-bathyal zone, based on benthic foraminifers (cf. Maiya et al., 1982).

USA, Alaska

Sitkalidak Formation: This formation is of Eocene to Oligocene age and occurs in a series of patches at the southeastern tips of points on Kodiak, Sitkalidak, and Sitkinak Islands. It is a rather uniform, about 3000 m-thick sequence of graded sandstone and siltstone beds, with a few conglomerate beds (Moore, 1969). The new species *Archivesica georgemoorei* was found near the top of the Sitkalidak Formation in the type area on the north shore near the east end of Sitkalidak Island (Figure 3), where it co-occurred with the thalassinid shrimp *Callianassa* aff. *porterensis* (cf. Moore, 1969). The dating of this site is somewhat uncertain, because it is solely based on the lithological similarities between the Sitkalidak Formation, the Burls Creek member of the Katalla Formation (Alaska), and the Blakeley Formation (Oregon) (F. S. MacNeil, written communication to G. W. Moore, 13 Aug. 1963). The fossil site is most likely a hydrocarbon-seep deposit (Goedert et al., 2003).

USA, Washington State

Astoria Formation: This formation crops out on the north shore (Washington) and south shore (Oregon) of the Columbia River. In Washington, rocks referred to as Astoria Formation in Pacific and Wahkiakum counties are 750 to 1000 m in thickness, and consist of thick-bedded, coarse-grained grayish-brown marine sandstone and soft, dark-gray siltstone (Moore, 1963; Wolfe & McKee, 1972; Wells, 1989). The new species

Isorropodon frankfortensis was recovered by acid etching from two small blocks of cold-seep carbonate found as float on beach terraces near the abandoned settlement of Frankfort (Figure 4F). The type locality of *Isorropodon frankfortensis* is equivalent to locality M-25 of Wolfe & McKee (1972) and USGS loc. M2790. Wolfe & McKee (1972) noted that the sediments in this area were deposited at a depth between 16 and 650 m.

Humptulips Formation: This formation crops out on the southwestern slope of the Olympic Mountains (Figure 4A), is approximately 1000 m thick (Rau, 1986), and is of late middle Eocene age (Prothero et al., 2001). It consists of siltstone and mudstone, and beds of structureless sandy siltstone, deposited at depths estimated to have been between 1500 and 2000 m (Rau, 1986). Several seep carbonates have been reported from this formation, containing, among other fossils, *Calyptogena chinookensis* and *Vesicomya* sp. (Squires & Goedert, 1991, 1996; Goedert & Kaler, 1996). The latter species is here described as *Archivesica* cf. *tschudi* (Olsson, 1931). The new material was found in a small seep limestone block on a gravel bar in the East Fork of the Humptulips River, approximately 400 m west and 600 m north of the southeast corner of Sec. 6, T20N, R9W, Grays Harbor County, Washington. The source of this material is likely the high cliff just upstream and on the south side of the river at the sharp bend, either allochthonous cold-seep limestone, or an *in situ* seep deposit. Additional specimens are from seep carbonate at CSUN loc. 1583.

Lincoln Creek Formation: This formation is an approximately 3000 m thick sequence of deep-water mud- and siltstones of late Eocene to early Miocene age, that crops out in western Washington State, between the southern slopes of the Olympic Mountains and the Columbia River. *Archivesica knapptonensis* n. sp. is from two late Oligocene seep-carbonate outcrops of the Lincoln Creek Formation. Blocks of seep carbonate were collected on tidal terraces near Knapp-ton on the north shore of the Columbia River at LACMIP loc. 5843 (Figure 4E). The age of this locality was considered early Miocene by Moore (1984) and late Oligocene by Goedert & Squires (1993). The vertebrate assemblage of this locality indicates that late Oligocene is the more probable age of these sediments (Barnes & Goedert, 2001; and J. L. Goedert, personal communication 2005). The mollusk fauna indicates a depositional depth of 100 to 350 m, whereas benthic foraminifers indicate 300 to 1000 m depth (Moore, 1984). At another site (Figure 4B, referred to as 'Canyon River site' herein) occur carbonate 'blebs' with small mollusks and a very large bivalve (*Cryptolucina*?) on a low bench on the east side of the Canyon River, approximately 40 m north and 260 m east of the

southwest corner of Sec. 25, R7W, T21N, Grays Harbor County. This site is of Oligocene age. A locality on the Satsop River (Figure 4C; LACMIP loc. 17747b; Oligocene) yielded a specimen of *Pliocardia?* sp. with a drill hole. Seep-related mollusks were described from two other carbonate blocks from that site by Kiel (2006), who also provided more details about the locality.

Siltstone of Cliff Point: Deep-water siltstones crop out on the north shore of the Columbia River, to the west of the Lincoln Creek Formation. Wells (1989) stated that this unit may be correlative with the 'Siltstone of Unit B' of Wolfe & McKee (1972). The 'Siltstone of Unit B' was deposited at depths between 300 and 1,000 m (Wolfe & McKee, 1972). A large seep carbonate in this formation at LACMIP loc. 5802 (Figure 4D) is the type locality of '*Calyptogena chinookensis*' Squires & Goedert, 1991. The hinge dentition of two specimens from this site is described to clarify its systematic position.

SYSTEMATIC DESCRIPTIONS

Family VESICOMYIDAE Dall & Simpson, 1901

Remarks: The Vesicomylidae are used here in the traditional sense. Based on anatomical and conchological observations on Recent North Atlantic species of *Kelliella* Sars, 1870 and *Vesicomya* Dall, 1886, Allen (2001) suggested that the Vesicomylidae should be synonymized with Kelliellidae. However, Cosel & Salas (2001) noted that Allen (2001) had misidentified some of his *Kelliella* species and pointed out distinctive differences between *Kelliella* and *Vesicomya*; hence, retaining the name Vesicomylidae.

The various genera related to *Calyptogena* Dall, 1891 are currently used very differently in the literature. On one end of the spectrum, Coan et al. (2000) treated *Calyptogena* as a subgenus of *Vesicomya*; *Akebiconcha*, Kuroda, 1943, *Archivesica* Dall, 1908, *Ectenagena* Woodring, 1938, and *Phreagena* Woodring, 1938 were considered synonyms of *Calyptogena*. On the other end of the spectrum, Keen (1969) considered all hitherto proposed names valid, except for *Adulomya* Kuroda, 1931, which was erroneously placed in the Solemyidae. Based on a combination of conchological and molecular data, Okutani et al. (2000) and Sasaki et al. (2005) recognized three subgenera of *Calyptogena*: *Calyptogena* s.s., *Archivesica*, and *Ectenagena*. This classification scheme is largely followed here, with the modifications that *Ectenagena* is shown here to be a junior synonym of *Adulomya*. The latter and *Archivesica* are considered herein to be independent genera.

We provide translated and emended generic diagnoses for these genera, based on our own observa-

tions. Figure 5 shows the main hinge features that characterize these genera. Table 1 gives an overview of their synonymies. We provide a list of the fossil species that we consider to belong to each of the genera; however, a full revision of the Recent species is beyond the scope of this study.

Genus *Hubertschenckia* Takeda, 1953

Hubertschenckia Takeda, 1953:85.

Type species: *Tapes ezoensis* Yokoyama, 1890 (by monotypy); Poronai Formation, upper Eocene, Hokkaido, Japan.

Taxonomic history: *Hubertschenckia ezoensis* was initially described by Yokoyama (1890) from "Cretaceous" deposits (=Eocene Poronai Formation) around Poronai on Hokkaido, and placed in the venerid genus *Tapes* Mühlfeld, 1811. Minato & Uozumi (1951) were the first who illustrated the hinge dentition of a left valve and noticed that this hinge resembles that of *Akebiconcha* Kuroda, 1943. Following the advice given to them by Dr. Tokubei Kuroda, they placed the species in the Veneridae and suggested that it may belong to a new genus.

When Takeda (1953) eventually proposed *Hubertschenckia* based on *Tapes ezoensis*, he placed it in the Veneridae and indicated a late Oligocene age for the Poronai Formation. He re-illustrated the figure of the left valve hinge provided by Minato & Uozumi (1951) and described the hinge structure as follows: 1) presence of laterals, 2) diminishing of anterior cardinal, 3) bifid middle cardinal in the right valve, 4) fusion of anterior lateral with cardinal tooth in the left valve. However, his description of the hinge dentition of the right valve was taken mainly from notes provided to him by Dr. Takumi Nagao, and he erroneously described the anterior cardinal teeth (2a, 3a) as anterior lateral teeth. Moreover, the bifid tooth in the right valve is the posterior cardinal one (3b), not the middle one. Oyama et al. (1960) also placed *Hubertschenckia* in the Veneridae. Keen (1969) illustrated the same specimen as Minato & Uozumi (1951) and Takeda (1953), followed Takeda's description, and placed *Hubertschenckia* in the Vesicomylidae. Subsequent workers have followed this placement (Kanno, 1971; Habe, 1977; Boss & Turner, 1980; Krylova & Sahling, 2006). Also Keen (1969) gave the stratigraphic age as Oligocene, following Takeda (1953). Then, Kaiho (1983, 1984) assigned the age of Poronai Formation to the late Eocene. Kanno & Teshima (1994) described *Hubertschenckia ezoensis* again and mentioned the following characteristics: 1) thin anterior cardinal tooth of left valve along dorsal margin, connecting with the middle tooth under the umbo, 2) existence of a subumbonal pit in juvenile specimens, but not developed in

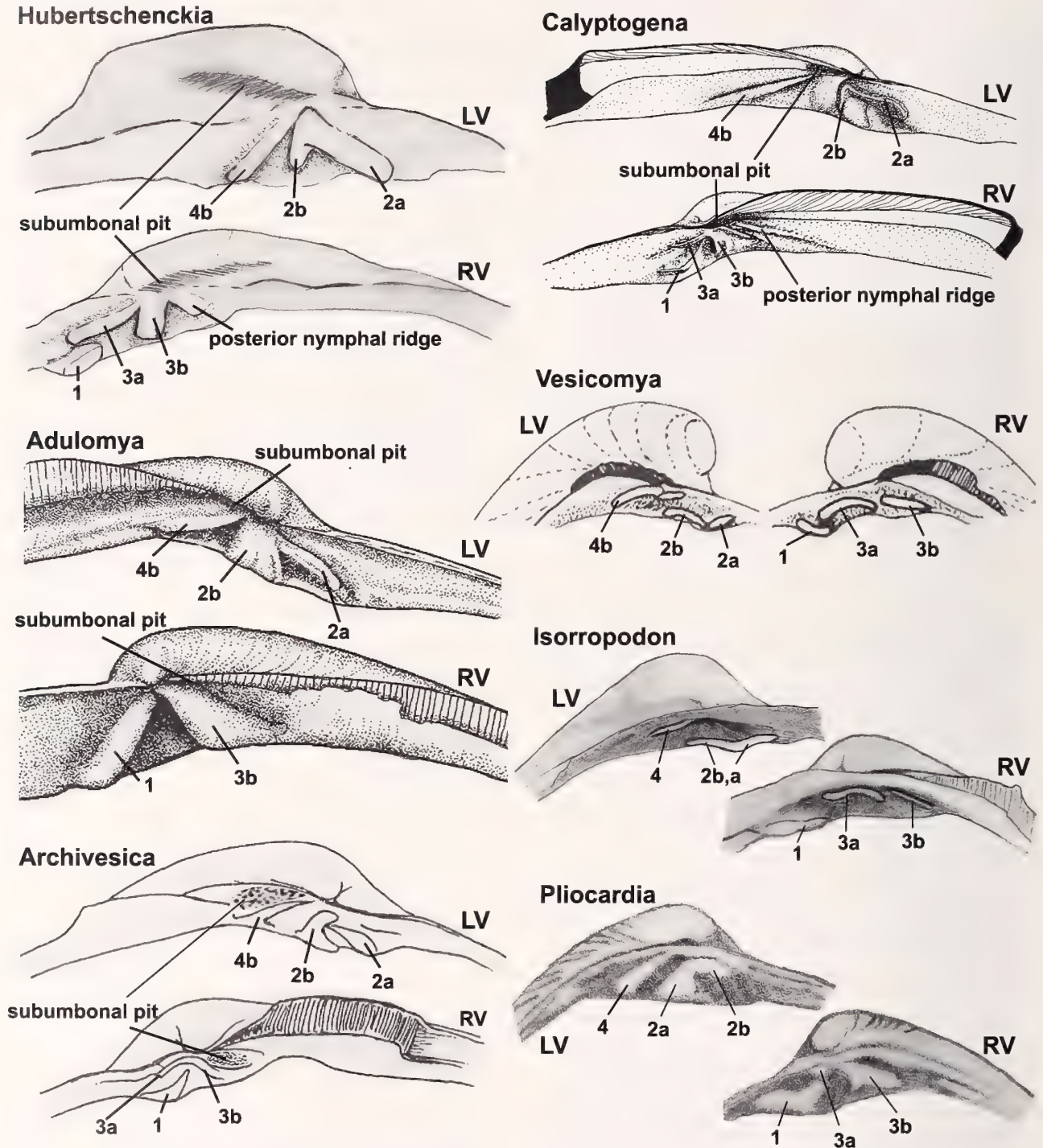


Figure 5. Terminology of the main hinge characters used in the text; not to scale. Sources: *Hubertschenckia* drawn from the specimens figured herein on Figures 6–7; *Adulomya* from Boss & Turner (1980:fig. 10E, of the holotype of *Adulomya elongata*); *Archivesica* from Okutani et al. (2000:fig. 12, which is based on specimen L99264A1-54 of *Archivesica gigas* provided by the Monterrey Bay Aquarium Research Institute); *Calyptogena* from Krylova & Sahling (2006:fig. 2, source not specified); *Vesicomya* from Cosel & Salas (2001:figs. 76–77, based on a specimen of *Vesicomya adamsi* collected off Namibia); *Isorropodon* redrawn from specimens of *Isorropodon perplexum* figured by Cosel & Salas (2001:figs. 44 and 47); *Pliocardia* redrawn from Woodring's (1925, pl. 20, figs. 3 and 5) figures of *Pliocardia bowdeniana*.

Table 1
Type species and synonymies of the genera used herein.

Genus	Type species	Synonyms
<i>Aduloma</i> Kuroda, 1931:27.	<i>Adulomya uchimuraensis</i> Kuroda, 1931	<i>Ectenagena</i> Woodring, 1938:51. ? <i>Pleurophopsis</i> Van Winkle, 1919:23.
<i>Archivesica</i> Dall, 1908:418.	<i>Callocardia gigas</i> Dall, 1896	<i>Akebiconcha</i> Kuroda, 1943:17. <i>Phreagena</i> Woodring, 1938:50.
<i>Hubertschenckia</i> Takeda, 1953:85.	<i>Tapes ezoensis</i> Yokoyama, 1890	
<i>Isorropodon</i> Sturany, 1896:17.	<i>Isorropodon perplexum</i> Sturany, 1896	
<i>Pliocardia</i> Woodring, 1925:147.	<i>Anomalocardia bowdeniana</i> Woodring, 1903	

adults, 3) existence of a pallial sinus throughout the entire ontogeny, suggesting an infaunal mode of life. This characterization agrees with our observations, except that the subumbonal pit can in fact also be observed in adult specimens.

Remarks: *Archivesica* is most closely related to *Hubertschenckia* in having a bifid posterior cardinal tooth (3b) in the right valve, a subumbonal pit, and a shallow pallial sinus. However, the hinge dentition of *Hubertschenckia* is more primitive than in *Archivesica* from the viewpoint of evolutionary change of the heterodont hinge (Cox et al., 1969). *Hubertschenckia* has a long anterior cardinal tooth (3a), a long central tooth (1) along basal margin of hinge, and a stout vertical posterior one (3b) in the right valve. *Hubertschenckia* shares with *Calypptogena* the posterior nymphal ridge and the posterior cardinal (3b) that points in an anteroventral direction.

Hubertschenckia ezoensis (Yokoyama, 1890)

(Figures 6–12)

Tapes ezoensis Yokoyama, 1890:197, pl. 25, figs. 6–8.
Tapes (new gen.?) *ezoensis* Yokoyama. Minato & Uozumi, 1951:150, pl. 13, figs. 108a–c.
Hubertschenckia ezoensis (Yokoyama). Takeda, 1953:85, pl.13, fig. 5; Oyama et al., 1960:188–189, pl. 58, figs. 2a–d.
non Meretrix (Macrocallista) ezoensis (Yokoyama). Yokoyama, 1928:77, pl. 8, fig. 1.
non Hubertschenckia ezoensis (Yokoyama). Honda, 1989:79, figs. 13, 14.

Material: Seventeen specimens from the Poronai Formation at Yayoi, Mikasa City, Hokkaido. For measurements of shell length, height and thickness see Table 2.

Type locality: Poronai, Mikasa City, Hokkaido.

Type material: Yokoyama (1890) did not designate a holotype. He mentioned that ‘several’ specimens were available, figured three of them, and made no

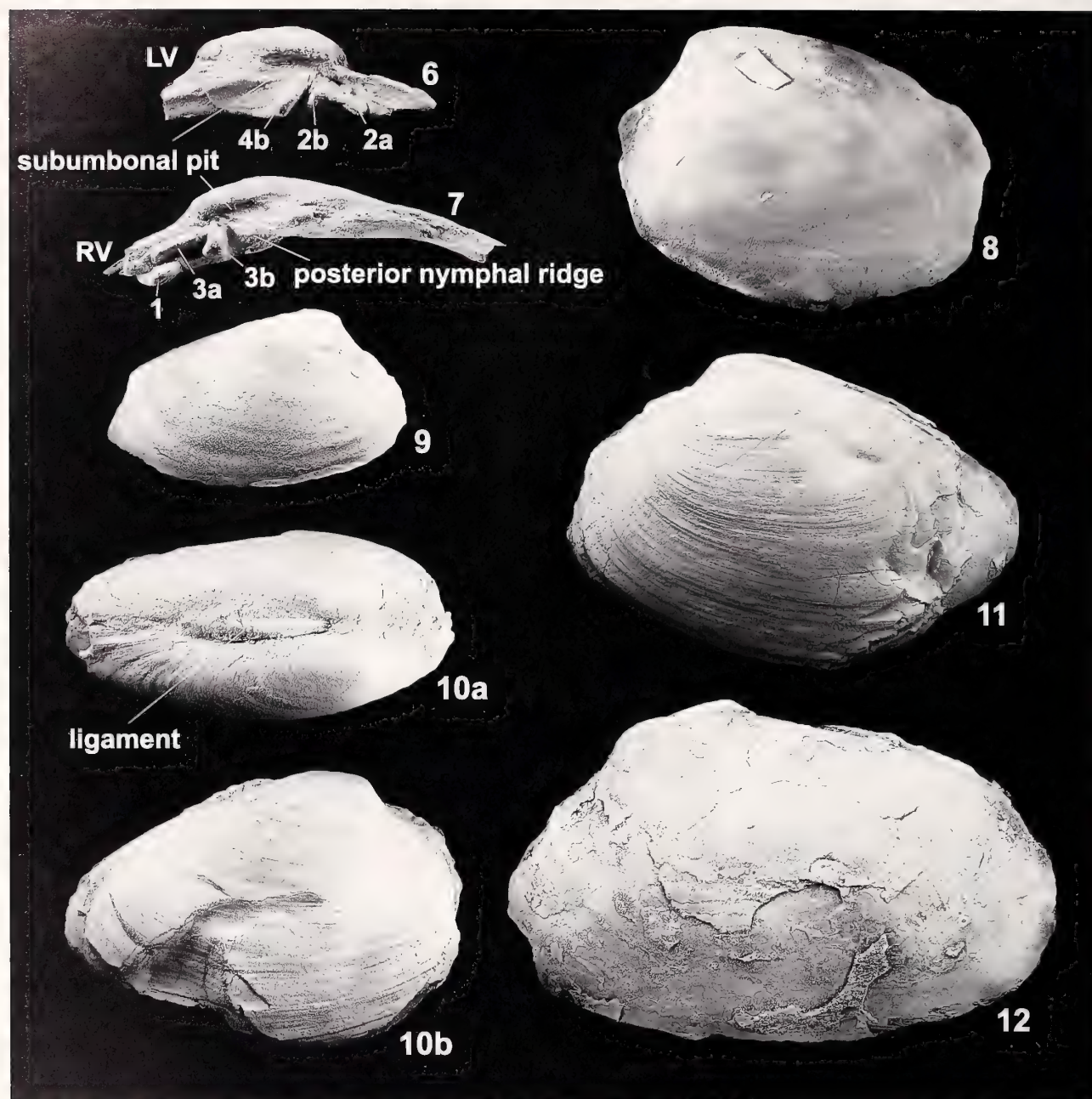
indications as to their repository. At the time of writing his report, Matajiro Yokoyama was based in Munich, Germany, and the specimens may have been deposited in the Bavarian State Collection. However, they could not be located there (A. Nützel, personal communication 2007), and may either have never been deposited there, or were destroyed during World War II. Takeda (1953, p. 86) indicated that the holotype is ‘preserved in Tokyo University,’ where it could not be located (T. Sasaki, personal communication 2007), and that a syntype from the collection of Dr. Satoru Uozumi is deposited as UH. Reg. No. 11181 at Hokkaido University in Sapporo. Because the holotype could neither be located in Munich nor in Tokyo, it is considered lost and we designate the specimen UH. Reg. No. 11181 as neotype.

Original description (translated from the German by SK):

“We have several specimens, but with only partly preserved shell. Shell thick, moderately convex, elongate elliptical, strongly inequivalved; posterior side approximately 2 ½ times as long as anterior side. Anterior and posterior margins rounded; ventral margin only slightly convex, almost parallel to hinge. Beaks small, pointed, curved, almost touching each other. The surface shows only irregular, concentric growth lines. The anterior muscle attachment scar is pear-shaped, the posterior one rounded. Sinus finger-

Table 2
Measurements of *Hubertschenckia ezoensis* specimens.

No. of specimens	Length (mm)	Height (mm)	Thickness (mm)
JUE no. 15837-1	74.6	43.7	29.3
JUE no. 15837-2	73.0	41.1	28.4
JUE no. 15837-3	72.8	40.0	32.6
JUE no. 15837-4	65.3	39.0	29.0
JUE no. 15837-5	56.7	29.1	24.1
JUE no. 15837-6	50.9	32.1	22.4
JUE no. 15837-7	35.4	24.5	17.1
JUE no. 15837-8	27.2	17.4	10.2
JUE no. 15837-9	17.6	10.0	8.1



Figures 6–12. *Hubertschenkia ezoensis* (Yokoyama). Figure 6. Left-valve hinge, hinge length 14.8 mm, JUE no. 15837-11. Figure 7. Right-valve hinge, hinge length 29.7 mm, JUE no. 15837-12. Figures 8, 9. Pallial sinus of both valves; Figure 8, length 43.6 mm+, JUE no. 15837-10; Figure 9, length 17.6 mm, JUE no. 15837-9. Figures 10–12. Outline of shells; Figure 10a, dorsal view showing long external ligament, Figure 10b, lateral view, length 35.4, JUE no. 15837-7; Figure 11, length 50.9 mm, JUE no. 15837-6; Figure 12, length 74.6 mm, JUE no. 15837-1.

shaped, approximately as deep as wide. Pallial line entire. The hinge dentition could not be examined fully. One specimen shows that the central of the three teeth of the right valve is bifurcated. A rather well-preserved specimen is 65 long and 40 mm high. Another, which is damaged at both ends, is 32 mm thick and 45 mm high.

The interior of the shell shows radial striations, which are well-visible in worn specimens" (Yokoyama, 1890).

Redescription: Shell of moderate size, attaining 74.6 mm length; shell outline elliptical, moderately inflated, equivalve and inequilateral, sculptured by

irregular growth lines. Beak prosogyrate, situated at anterior fifth of shell. Anterodorsal margin broadly arched, graduating into rather straight and oblique anterior margin; ventral margin broadly arcuate; postero-dorsal margin nearly straight, forming obtuse angle with rounded posterior margin. Escutcheon demarcated by blunt ridge running from beak to posterior end; lunule absent. External ligament strong and occupying two-fifths of posterior length.

Hinge plate rather wide, with three cardinal teeth in each valve. Right valve hinge: anterior cardinal tooth (3a) long, parallel to dorsal margin; posterior cardinal tooth (3b) vertical, stout, bifid, connected to anterior tooth above central tooth; area behind posterior cardinal tooth deeply excavated; posterior nymphal ridge low but distinct; central tooth (1) thin and long, nearly parallel to the anterior one, inserting its top under dorsal teeth (3a, b); subumbonal pit long and shallow just below umbo. Left valve hinge: anterior tooth (2a) long, parallel to antero-dorsal margin, connected to short central tooth (2b); posterior tooth (4b) thin, oblique posteriorly, separated from central tooth by deep groove; subumbonal pit deeply excavated, situated above posterior tooth.

Anterior muscle scar subcircular; posterior one pear-shaped; pallial sinus shallow, as wide as deep; strong ridge running from beak to deepest point of pallial sinus; radial interior striae rather weak.

Comparison: *Hubertschenckia* is currently only known from its type species *H. ezoensis*. The most closely related species are found in the genus *Archivesica*: *A. kawamurai* (Kuroda, 1943) and *A. georgemoorei* n. sp. described herein. *Hubertschenckia ezoensis* resembles *A. kawamurai* in having a bifid posterior cardinal tooth and a thin anterior cardinal tooth along the dorsal margin in the right valve, and in the existence of subumbonal pit and a shallow pallial sinus. However, *A. kawamurai* differs from *H. ezoensis* in having a more vertical central tooth (1) and a shorter anterior cardinal tooth (3a) in the right valve, a longer and anteriorly inclined central tooth (2b) and a shorter posterior tooth (4b) in the left valve; a smaller and deeper subumbonal pit, and strongly impressed radiating interior striae. The extant species *Archivesica solidissima* (Okutani, Hashimoto & Fujikura, 1992) was recently synonymized with *A. kawamurai* based mainly on molecular data (Kojima et al., 2006).

The hinge of *Archivesica georgemoorei* resembles that of *H. ezoensis* in having a bifid posterior cardinal tooth in the right valve (3b) and a thick anterior cardinal (1) parallel to the dorsal shell margin. It differs significantly, however; in having a more posteriorly directed posterior cardinal (3) in the right valve, and a thinner posterior cardinal (4), a smaller anterior cardinal (2) in

the left valve, and the nymph is shorter in *Archivesica georgemoorei*.

Remarks: Yokoyama (1928) described *Meretrix (Macrocallista) ezoensis* (Yokoyama) from the Pliocene-Pleistocene "upper Byoritsu Bed" in Taiwan. However, as noted by Takeda (1953), the hinge and shell morphology is distinctly different from *Hubertschenckia ezoensis*. Honda (1989) described two articulated specimens from an *Ostrea*-bearing sandstone of the Eocene Shitakara Formation in eastern Hokkaido as *Hubertschenckia ezoensis*, but did not illustrate their hinge structures. From their mode of occurrence, we infer that these specimens were shallow water-dwelling venerids rather than vesicomyids.

Distribution: Upper Eocene Poronai Formation in the Yubari coal-field, central Hokkaido; upper Eocene? Tappu Formation in the Uryu coal-field, northwestern Hokkaido (Ôhara & Kanno, 1969, 1973); upper Eocene Omagari Formation and lower Oligocene Nuibetsu Formation (Takeda, 1953) in the Kushiro coal-field, eastern Hokkaido.

Genus *Adulomya* Kuroda, 1931

?*Pleurophopsis* Van Winkle, 1919:23.

Adulomya Kuroda, 1931:27.

Ectenagena Woodring, 1938:51.

Type species: *Adulomya uchimuraensis* Kuroda, 1931 (by monotypy); Miocene Bessho Formation, central Honshu, Japan.

Redefinition: Shell thin, large, elongate or cylindrical, ventral margin concave or almost straight; both ends rounded; beaks prosogyrate, situated anteriorly; surface with coarse, concentric growth increments. Inner surface with deep anterior muscle scar bounded by a deep groove; posterior muscle scar indistinct. Interior of ventral margin thick, with numerous fine radial riblets. Ligament external and long. Left valve with strong posterior cardinal (4b) parallel or oblique to posterior shell margin; anterior cardinal strong, 2b points ventrally, 2a parallel or subparallel to the antero-dorsal margin; nymph short. Right valve with two cardinals, anterior tooth (1) weaker than posterior one, pointing in an antero-ventral direction, posterior tooth (3b) pointing in a postero-ventral direction. Subumbonal pit in both valves present or in some cases absent (modified from Kanno et al., 1998).

Remarks: Because he had only a few articulated specimens at hand, Kuroda (1931) erroneously described *Adulomya uchimuraensis* as edentulous and consequently placed the genus in the protobranch family Solemyidae Adams & Adams, 1857. When Kanno & Ogawa (1964) allocated *Adulomya chitanii*

Kanehara, 1937 to *Akebiconcha* (= *Archivesica*), they emphasized the edentulous hinge of *A. uchimuraensis*. *Adulomya* was subsequently treated as solemyid by Kamada (1962), Cox et al. (1969), and Boss & Turner (1980), among others.

However, Habe (1977) had already described the strong cardinal teeth and the absence of a pallial sinus in *A. uchimuraensis* and placed *Adulomya* in the Vesicomidae. Kanno et al. (1998) used many newly collected specimens of *Adulomya uchimuraensis* from one of the localities described by Kuroda (1931) to redefine *Adulomya*. They pointed out that *Adulomya* shares almost all its characters with *Ectenagena*, but differs by its subumbonal pit which is present throughout the entire ontogeny of the shell, whereas in *Ectenagena* the subumbonal pit is supposedly present only in juveniles. This distinction, however, is doubtful. The holotype of *Calypptogena elongata* Dall, 1916, type species of *Ectenagena* has a subumbonal pit judging from the figures provided by Boss (1968). Kanno et al. (1998) noted that the holotype with a shell length of 43 mm is a young specimen, but Coan et al. (2000) gave its maximum length as 50 mm. Thus, *Ectenagena* is here regarded as a synonym of *Adulomya*.

Pleurophopsis Van Winkle, 1919, from the middle Miocene of Trinidad (Caribbean) resembles *Adulomya* in all known characters, but its type species *P. unioides* Van Winkle, 1919, is only known from incomplete specimens that lack crucial characters including cardinal tooth 3b, escutcheon, and nymph. Therefore the name *Pleurophopsis* should not be used (Kiel, 2007). Other species assigned or referred to *Pleurophopsis* may be vesicomids, but do not belong to *Adulomya* (Kiel & Peckmann, in press).

Archivesica resembles *Adulomya* in having three radiating cardinal teeth in the left valve and a subumbonal pit. It differs from *Adulomya* by having a narrow hinge plate, three cardinal teeth in the right valve, and a shallow pallial sinus. *Calypptogena* (s.s.) can easily be separated from *Adulomya* by its three cardinal teeth including a very stout right posterior one, and by the lack of a subumbonal pit.

Included fossil species: *Adulomya uchimuraensis* Kuroda, 1931, *Adulomya chitanii* Kanehara, 1937, *Calypptogena* (C.) *chinookensis* Squires & Goedert, 1991, and *Adulomya hokkaidoensis* Amano & Kiel, sp. nov.

Distribution: Recent species are known from vents and seeps in the northeastern Pacific (Coan et al., 2000; Desbruyères et al., 2006) and from seeps in the northwestern Pacific (Sasaki et al., 2005); fossil species are known from late Eocene seeps in Washington State (this study), from early to middle Miocene whale-falls in Japan (Amano & Little, 2005; Amano et al., 2007), and from a turbidity current deposit of early Oligocene

age in the Makah Formation in Washington State (Goedert & Squires, 1993).

Adulomya hokkaidoensis Amano & Kiel, sp. nov.

(Figures 13–18)

Calypptogena sp. Amano & Little, 2005:figs. 5 A, E, F.

Diagnosis: A medium-sized *Adulomya* with elongate shell, sculptured by rough concentric ridges; subumbonal pit very elongate; ligament exterior and short, two radiating cardinal teeth in right valve; left valve with three radiating teeth, middle one strongest.

Holotype: Length 46.2 mm, height 16.7 mm, JUE no. 15848.

Paratype: Length 59.4 mm, height 16.7 mm+, JUE no. 15849; Length 66.2 mm+, height 22.6 mm, JUE no. 15850.

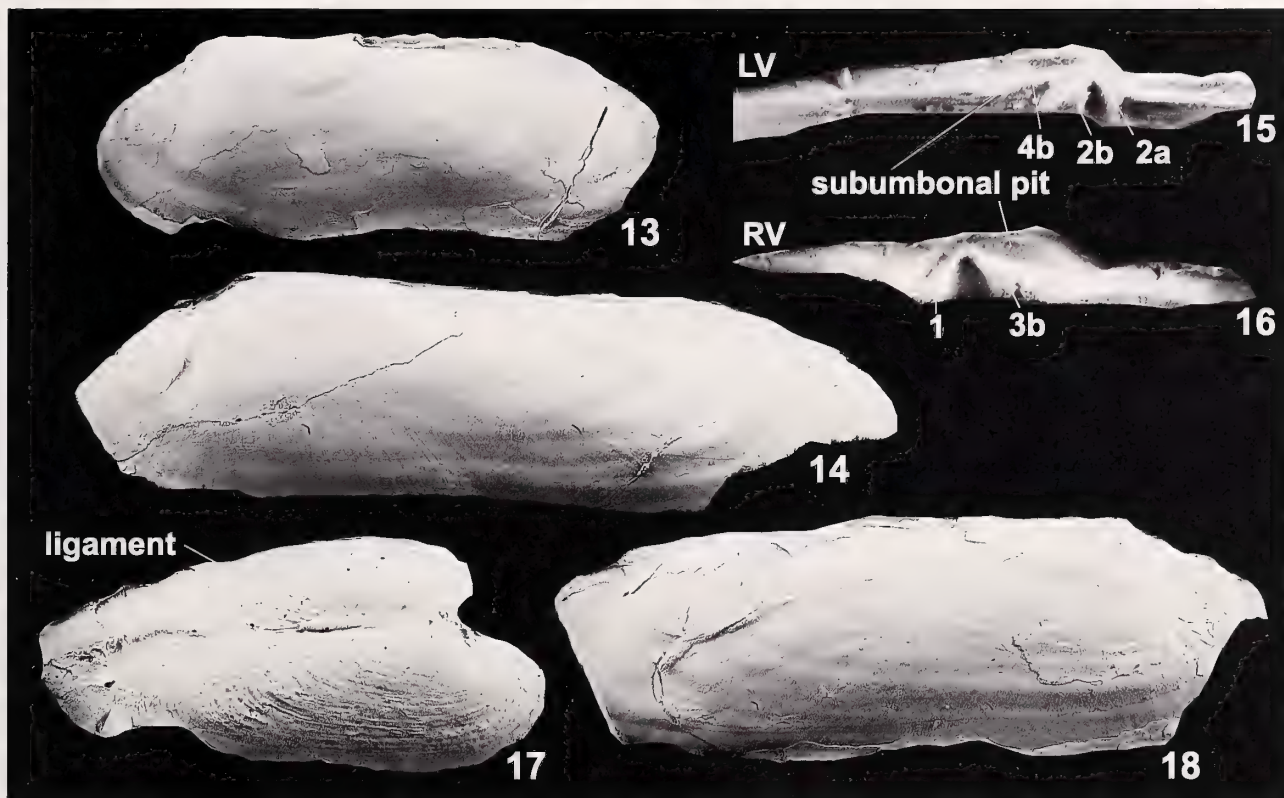
Type locality: Large road side cliff along the Setakinai River, 5.5 km upstream from Shosanbetsu Village, Hokkaido; lower middle Miocene Chikubutsu Formation.

Description: Shell of moderate size, more than 66.2 mm long, thin-walled, elongate, equivalve and inequilateral, weakly inflated, sculptured by few rough concentric ridges on posterior part, growth lines cover the entire surface. Beak prosogyrate, situated at anterior fifth of shell. Antero-dorsal margin broadly arched, graduating into rounded anterior margin; ventral margin straight and slightly excavated at middle portion; postero-dorsal margin nearly straight, parallel to ventral margin, graduating into rounded posterior margin. Escutcheon and lunule absent; ligament exterior, weak and short.

Hinge plate narrow, with two cardinals in right valve and three cardinals in left valve. Right valve hinge: anterior cardinal tooth (3a) reduced; posterior cardinal tooth (3b) slightly bifid, oblique posteriorly; central tooth (1) thin, anteriorly slightly oblique; subumbonal pit long and shallow just below umbo. Left valve hinge: anterior tooth (2a) thin, slightly oblique anteriorly, connected to stout middle tooth (2b); posterior tooth (4b) very thin, oblique posteriorly; subumbonal pit shallow, situated above posterior tooth.

Anterior muscle scar subcircular; posterior one ovate; pallial sinus absent; deep groove running just under posterior muscle scar; radial interior striae distinct.

Comparison: The extant species *Adulomya elongata* (Dall, 1916) resembles *A. hokkaidoensis* in having a thin and compressed shell with two cardinal teeth in the



Figures 13–18. *Adulomya hokkaidoensis* sp. nov. Figure 13. Holotype, length 46.2 mm, JUE no. 15848. Figure 14. Paratype, length 59.4 mm, with slightly broken ventral part, showing distinct radiating interior striae, JUE no. 15849. Figure 15. Rubber cast of left valve hinge of paratype (JUE no. 15849), hinge length 25.7 mm. Figure 16. Rubber cast of left valve hinge of paratype (JUE no. 15851), hinge length 16.5 mm. Figure 17. Paratype, dorsal view showing the short ligament, length of specimen 40.8 mm+, JUE no. 15852. Figure 18. Paratype showing entire pallial line and posterior adductor scar, length 66.2 mm+, JUE no. 15850.

right valve, a subumbonal pit and lacking a pallial sinus. However, its more elongate shape and the presence of concentric undulations on the posterior surface distinguish *A. hokkaidoensis* from *A. elongata*. The fossil *A. uchimuraensis* and the extant *A. phaseoliformis* (Métivier, Okutani & Ohta, 1986) have larger and more elongate shells.

Distribution: Known only from the whale-fall community at the type locality.

Etymology: For its occurrence on Hokkaido.

Adulomya chinookensis (Squires & Goedert, 1991)

(Figures 19–23)

Calyptogena n. sp. Goedert & Squires, 1990:figs. 2 o–p.

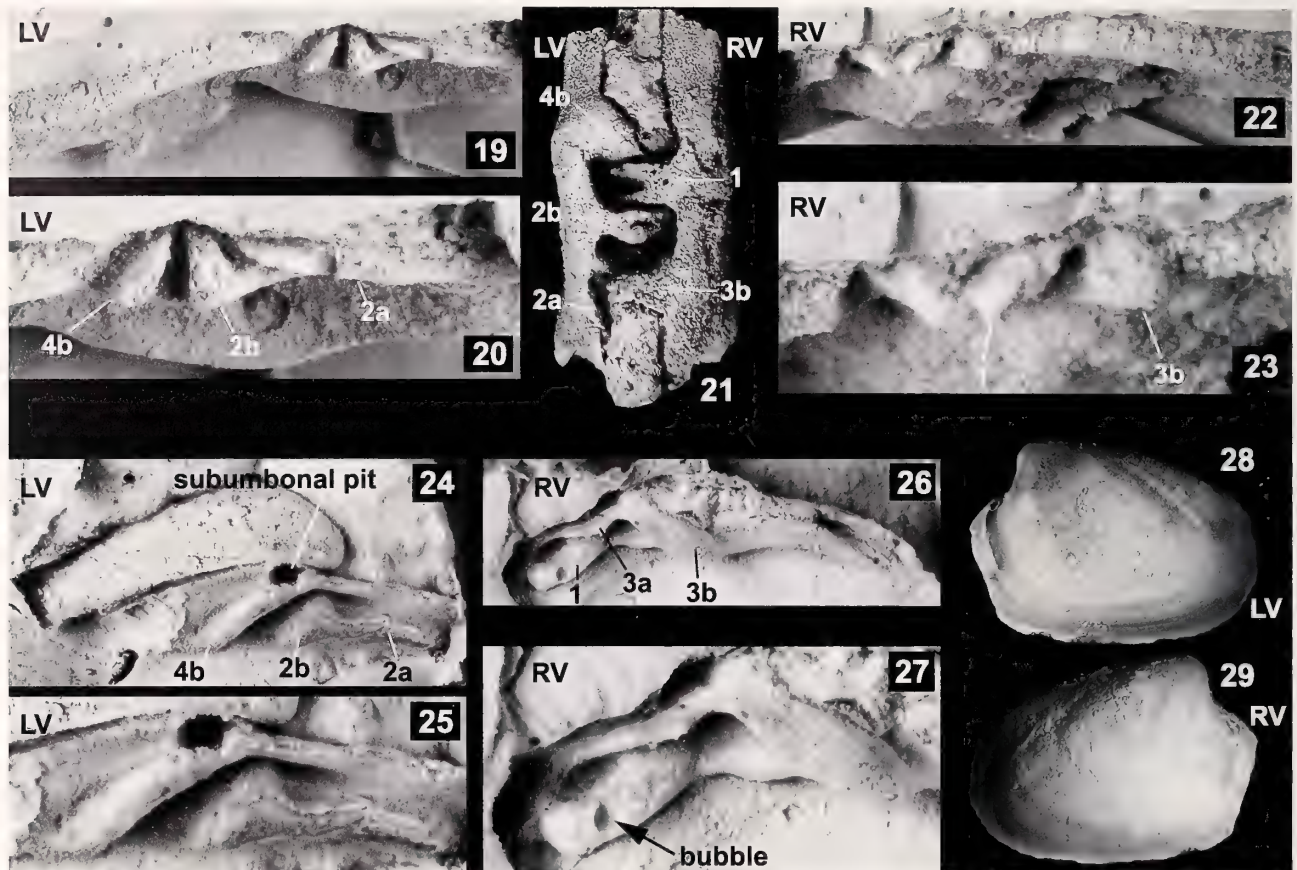
Calyptogena (*Calyptogena*) *chinookensis* Squires & Goedert, 1991:413–415, figs. 2.7–2.11; Goedert & Squires, 1993:74–76, fig. 3.

Vesicomya (*Calyptogena*) sp. Goedert et al., 2003:228, Pl. 42, figs. 6, 7.

non *Calyptogena* (*Calyptogena*) *chinookensis* Squires & Goedert. Goedert & Squires, 1993:fig. 4.

Supplementary description: Left-valve hinge with strong posterior cardinal (4b) pointing in postero-ventral direction, slightly tapering at its dorsal side; cardinal 2b solid, same length as cardinal 4b, pointing in ventral direction, anterior cardinal 2a detached from 2b, thinner than the other cardinals, elongate, and pointing in anterior direction. Right valve hinge with two cardinals, middle cardinal 1 elongate-lenticular, pointing in anterior direction, posterior cardinal 3b strong, bifid, peg-like, pointing in ventral direction. Pallial line entire, starting at postero-ventral end of anterior adductor scar, distant from ventral margin (ca. 22% of shell height below umbo, 44% at posterior turning point), no pallial sinus but pallial line merges with the elongate posterior adductor scar.

Remarks: Specimens previously assigned to *Calyptogena* (*Calyptogena*) *chinookensis* from various formations apparently belong to more than one species. Figures 19, 20, 22, and 23 show a silicone rubber cast of an internal mold of a specimen from the type locality at Bear River (LACMIP loc. 5802), which we consider to represent the ‘true’ *chinookensis*. Its right valve hinge



Figures 19–29. *Adulomya chinookensis* (Squires & Goedert, 1991) from the type locality at Bear River, Washington State, USA (LACMIP loc. 5802). Figures 19–20. Rubber cast of a steinkern (USNM 534948), left valve. Length of section shown in Figure 19: 24.0 mm; close-up in Figure 20: 13.0 mm. Figure 21. Ventral view of a complete, articulated hinge, length 14.0 mm (USNM 534949). Figures 22–23. Right valve of same rubber cast as in Figures 19–20, length of section shown in Figure 22: 24.0 mm, close-up in Figure 23: 11.0 mm.

Figures 24–29. *Archivesica cf. tschudi* (Olsson, 1931) from the Humptulips River, Washington State, USA. Figures 24–25. Rubber cast of an external mold of a left valve, note deep subumbonal pit, length of section shown in Figure 24: 12.0 mm, close-up in Figure 25: 8.0 mm (USNM 534950). Figures 26–27. Rubber cast of an external mold of a right valve, note that the round hole in the anterior side of cardinal 1 is a bubble in the rubber, not a shell feature. Length of section shown in Figure 26: 15.0 mm; close-up in Figure 27: 8.0 mm (USNM 534951). Figures 28–29. Steinkern from CSUN loc. 1583 showing pallial line and adductor scars, length 27.0 mm (USNM 534952).

differs from the late Oligocene specimen figured by Goedert & Squires (1993:fig. 4) because the cardinals 1 and 3 are not fused in the 'true' *chinookensis*, and cardinal 1 is more elongate than in Goedert & Squires's specimen. Additional material collected at the same site from which Goedert & Squires (1993) described their right valve showed that the corresponding left valve differs even more from that of the 'true' *chinookensis* by having a thick, roundish cardinal 2b and an elongate, thin cardinal 2a. The late Oligocene species to which the right valve figured by Goedert & Squires (1993:fig. 4) belongs, is described as *Archivesica knapptonensis* n. sp. below. Specimens described as *Vesicomya (Calypstogena)* sp. by Goedert et al. (2003) from the 'Whiskey Creek site' in the Pysht Formation (late Eocene,

Washington State) have the same hinge dentition as the Bear River specimens shown here, but have a stronger ridge from the umbo to the posterior adductor scar on the inner side of the shell.

Distribution: Upper Eocene informal 'Siltstone of Cliff Point' (i.e., Bear River deposit) and the 'Whiskey Creek site' in the Pysht Formation to the lower Oligocene Makah Formation, Washington State, USA. The species is probably more widely distributed in this area, but specimens with the same general shell outline apparently belong to different species and genera, and without the hinge, except at the type locality of *chinookensis*, we are unable to confirm any additional records.

Genus *Archivesica* Dall, 1908*Archivesica* Dall, 1908:418.*Phreagena* Woodring, 1938:50.*Akebiconcha* Kuroda, 1943:17.

Type species: *Callocardia gigas* Dall, 1896 (by original designation); Recent, Gulf of California.

Original diagnosis: Shell inflatedly modioliform, medially slightly constricted, with the hinge plate short and broad and the hinge teeth radially disposed; lunule not circumscribed by an impressed line; pallial line without a sinus, but descending nearly vertically from the middle of the posterior adductor scar (Dall, 1908, p. 418).

Emended diagnosis: Shell broadly oval to very elongate; sculpture of commarginal growth lines only; lunular incision present or absent; anterior adductor scar moderately deep impressed, anterior adductor scar only weakly impressed; pallial line with shallow sinus. Hinge of right valve with subumbonal pit; anterior cardinal tooth thin, parallel or somewhat oblique to antero-dorsal margin; middle cardinal tooth (1) as strong as 3a or much thicker, starting anywhere between underneath umbo; posterior cardinal tooth (3b) sometimes bifid, as strong as 3a or stronger, usually fused with 3a underneath umbo, either perpendicular to 3a or points in a more posterior direction. Hinge of left valve with subumbonal pit, anterior cardinal 2a elongate and thin, and parallel or subparallel to antero-dorsal margin; middle cardinal 2b stout, peg-like tooth of variable thickness; posterior cardinal 4b usually thin and long.

Comparison: *Calypptogena* differs from *Archivesica* by the presence of a nymphal ridge in the right valve, which *Archivesica* mostly lacks (Figure 5); by the lack of a subumbonal pit, which is present in *Archivesica*; by the orientation of the anterior branch of the cardinal tooth 3b, which points in a ventral or even anterior direction in *Calypptogena*, but points in a posterior direction in *Archivesica*; and by the large size of cardinal 3b of *Calypptogena* which is much smaller in *Archivesica*. Moreover, the shell size of *Calypptogena* is usually small (about 60 mm in maximum length) and does not exceed 90 mm (cf. Krylova and Sahling, 2006), whereas the maximum size of many Recent species of *Archivesica* exceeds 100 mm. *Adulomya* lacks an anterior cardinal 3a, which distinguishes it from *Archivesica*. *Hubertschenckia* differs from *Archivesica* by its much stronger cardinals 3a and 3b and also by the orientation of the anterior branch of the cardinal tooth 3b, which points in a ventral or slightly anterior direction. In *Archivesica*, 3b points in a posterior direction. The genus *Vesicomya* apparently consists of

small species from the Atlantic (Cosel & Salas, 2001), and differs from *Archivesica* in having much smaller, thinner, roundish shells (up to 13 mm in length), cardinal teeth parallel to the hinge line, no pallial sinus, and no subumbonal pit (e.g., Figure 5).

Remarks: Okutani et al. (2000) reviewed the nomenclatural history of *Archivesica*, largely agreed with Dall's original diagnosis, and agreed with Bernard (1974) that there may be a small pallial sinus. Here we provide a more detailed diagnosis of the configuration of the hinge teeth and show that there can be a lunular incision (= a groove between a non-depressed lunule and disc), contrary to Dall's diagnosis. Cosel & Salas (2001) showed for the vesicomylid genera *Vesicomya* and *Isorropodon* that the lunular incision can vary greatly in strength from nearly absent to deeply incised. We consider the presence or absence of a lunular incision insufficient to distinguish genera among the Vesicomylidae and emend Dall's diagnosis accordingly.

The molecular phylogenetic tree of vesicomylids of Kojima et al. (2004) derived from mitochondrial COI sequences included a monophyletic group of eight species that included *Archivesica gigas*, the type species of *Archivesica*, and *A. solidissima*, which was shown to be a synonym of *A. kawamurai* Kuroda, 1943 (Kojima et al., 2006), type species of *Akebiconcha* Kuroda, 1943. Thus we consider *Akebiconcha* to be a synonym of *Archivesica*. All eight taxa of this monophyletic group were assigned to *Archivesica* by Sasaki et al. (2005).

Woodring (1938) introduced *Phreagena* based on *P. lasia* Woodring, 1938 but later recommended to synonymize this genus with *Calypptogena* (cited in Winterer & Durham, 1962; Boss, 1968; and Boss & Turner, 1980). These authors as well as Squires (1991) followed this synonymization, but Krylova & Janssen (2006) attempted to revive *Phreagena* and suggested close phylogenetic relations to *Akebiconcha* and *Archivesica*. As outlined above, we consider *Akebiconcha* to be synonymous with *Archivesica*. Also *Phreagena lasia* shows (on the illustrations of Woodring, 1938, pl. 5, fig. 3; and Squires, 1991:fig. 8; and perhaps also of Krylova & Janssen, 2006, pl. 2, fig. 7) a bifurcating central cardinal 1, a character that we have not seen in our material of *Archivesica*. However, the central cardinal 2b in species of *Adulomya* may or may not bifurcate (compare figs. 4E–G of Boss & Turner, 1980). Also, in their diagnosis of *Phreagena*, Krylova & Janssen (2006, p. 237) wrote that cardinal 1 is 'sometimes bifid.' Thus we consider a bifurcating central cardinal 1 to be insufficient to distinguish genera among the Vesicomylidae and regard *Phreagena* as a synonym of *Archivesica*.

Included fossil species: *Archivesica georgemoorei* n. sp. (Oligocene?), *Archivesica knapptonensis* n. sp. (late Oligocene), *Archivesica* cf. *tschudi* (Olsson, 1931) (late

middle Eocene, see below), *Phreagena gibbera* Crickmay, 1929 (*P. lasia* Woodring, 1938 has been considered to be a junior synonym of *P. gibbera* by Squires, 1991; early Pliocene to middle Pleistocene), *Calyptogena nipponica* Oinomikado & Kanehara, 1938 (late Miocene to Pliocene), and *Akebiconcha kawamurai elongata* Ozaki, 1958 (late Pliocene).

Distribution: Recent species occur at vents and seeps in the Pacific (Scarlato, 1981; Coan et al., 2000; Sasaki et al., 2005), fossil species first appear at seeps in the late middle Eocene of Washington and are also known from seep deposits in California, Washington, Alaska, and Honshu (this study).

Archivesica cf. *tschudi* (Olsson, 1931)

(Figures 24–29)

Vesicomya sp. Squires & Goedert, 1996:270; Goedert & Kaler, 1996:67.

?*Vesicomya tschudi* Olsson, 1931:54, pl. 4., figs. 6, 8.

?*Vesicomya ramondi* Olsson, 1931:55, pl. 4, fig. 3.

?*Vesicomya* (*V.*) aff. *V. (V.) tschudi* Olsson. Squires & Gring, 1996:69, figs. 4.9–4.12.

Description: Shell small and ovate; postero-dorsal margin almost straight, angulate at transition to subtruncated posterior margin; ventral margin slightly arcuated. Umbo protruded above dorsal margin; beak situated anterior at one-seventh of shell length. Anterior adductor scar deeply impressed, pallial line starting at postero-ventral end of anterior adductor scar, moderately distant from ventral margin, no pallial sinus. Right valve with very strong middle cardinal (1), parallel to shell margin, slightly longer in anterior direction than anterior cardinal (3a); anterior cardinal (3a) thin, somewhat undulating, parallel to shell margin; posterior cardinal (3b) bifurcate, anterior branch slightly concave, as thin as 3a, posterior branch elongate-lenticular, almost as strong as cardinal (1),

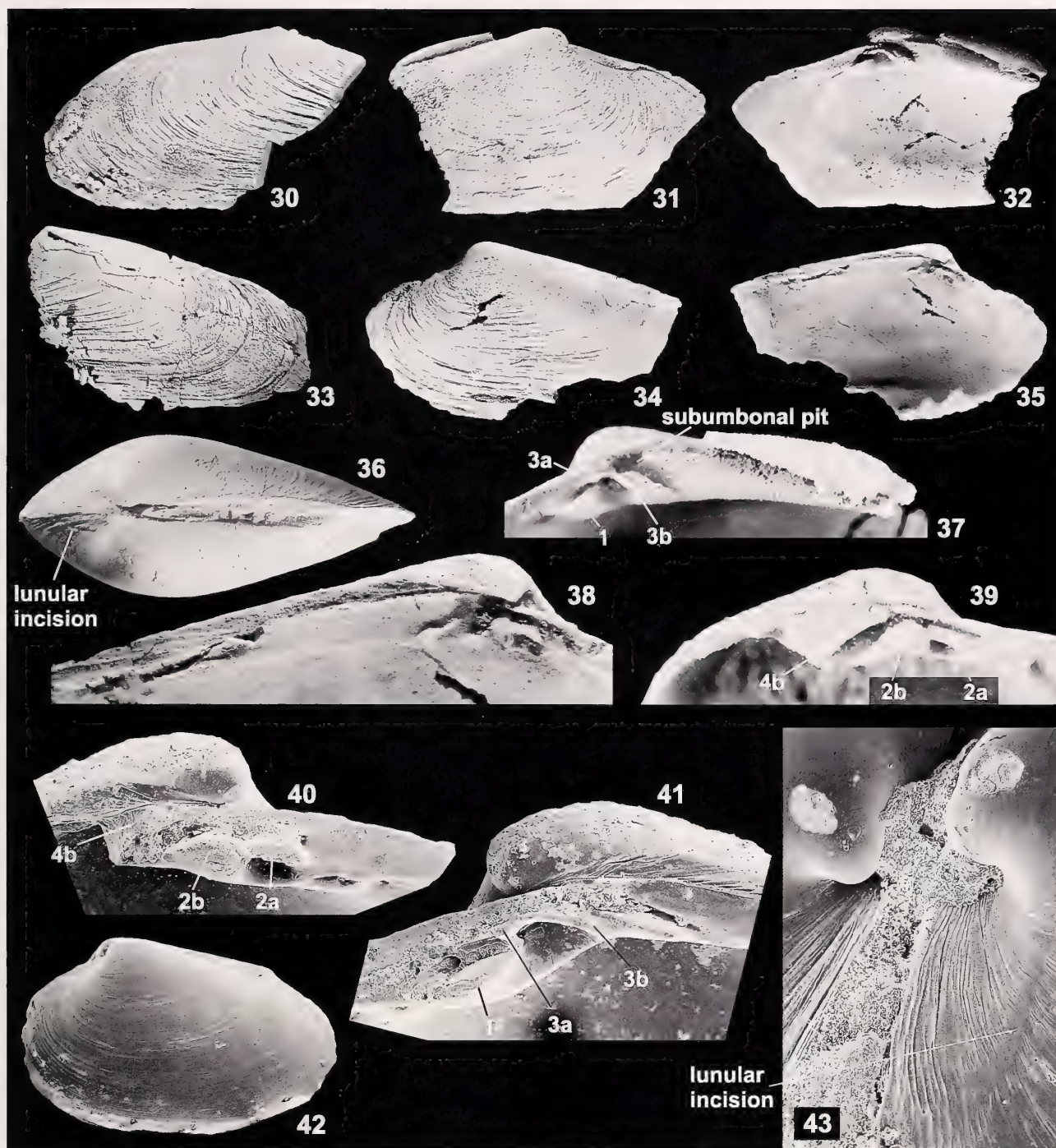
both branches point in a postero-ventral direction; nymph narrow, slightly shorter than hinge tooth area. Right valve with thin, elongate, undulating anterior cardinal (2a) parallel to shell margin, fused with cardinal 2b beneath umbo, 2b thick, short, comma-shaped, almost parallel to shell margin but slightly tilted in a ventral direction; posterior cardinal (4a) thin, straight, parallel to shell margin, fused with 4b just posterior of umbo, posterior cardinal 4b strong, elongate, slightly convex, pointing in a postero-ventral direction; subumbonal pit very deep and almost round.

Remarks: Our specimens show no difference in general shell shape and pallial-line characters to those described and illustrated as *V. tschudi* and *V. aff. tschudi* by Olsson (1931) and Squires & Gring (1996). Olsson (1931, p. 55) noted impressions of the hinge-line show two cardinal teeth in each valve and no laterals. This generally agrees with the observations on our material, but does neither allow an unequivocal recognition of, nor a clear distinction from, '*Vesicomya*' *tschudi*. Thus we describe the species here as *Archivesica* cf. *tschudi*. It is currently the oldest vesicomysid for which hinge dentition is known.

Olsson (1931) described *Vesicomya tschudi* and *Vesicomya ramondi* without discussing distinguishing features. According to his descriptions, *ramondi* has a pointed posterior margin, whereas that of *tschudi* is rounded. Squires & Gring (1996) noted that *ramondi* is more elongate than *tschudi*. However, Olsson's figures of *ramondi* (pl. 4, fig. 3) and his paratype of *tschudi* (pl. 4, fig. 8) show no discernable difference. Considering the intraspecific variability among our specimens from the Humptulips Formation, we think it is more likely that *tschudi* and *ramondi* are the same species.

Distribution: Humptulips Formation, Washington State, USA, upper middle Eocene (Squires & Goedert, 1996; herein). Specimens with identical shell shape but unknown hinge details were described as *Vesicomya* aff. *tschudi* from the upper Eocene Wagonwheel

Figures 30–43. *Archivesica knapptonensis* n. sp. from the upper Oligocene part of the Lincoln Creek Formation in Washington State, USA. Specimens on Figures 30–39 coated with ammonium chloride; specimens on Figures 40–43 coated with gold for SEM photography. Figure 30. Fragment of right valve, posterior side, from Knappton (LACMIP loc. 5843), length 18.0 mm (USNM 534953). Figures 31–32. Holotype, internal and external view of right valve, from Knappton (LACMIP loc. 5843), length 13.5 mm (USNM 534954). Figure 33. Fragment of posterior side of left valve, from Knappton (LACMIP loc. 5843), length 20.0 mm (USNM 534955). Figures 34–35. Paratype, internal and external view of left valve, from LACMIP loc. 5843, length 19.0 mm (USNM 534956). Figure 36. Ventral view of an articulated specimen, showing the well-developed lunular incision, from LACMIP loc. 17747b, length 23.0 mm (USNM 534957). Figure 37. Close-up of hinge dentition of holotype. Figure 38. Close-up on hinge dentition of paratype (same specimen as Figures 34–35). Figure 39. Close-up of hinge dentition of a left valve of a smaller specimen than in Figure 38, from LACMIP loc. 5843, length 11.0 mm (USNM 534958). Figures 40–43. Small specimens from the 'Canyon River site,' note that the posterior branch of the bifurcating cardinal 3b is more detached from 3a than in the larger specimens shown above. Figure 40. Close-up on hinge of left valve, length of section 2.1 mm (USNM 534959). Figure 41. Close-up of hinge of right valve, length of section 2.0 mm (USNM 534960). Figure 42. Left valve of articulated specimen, length 5.3 mm (USNM 534961). Figure 43. Close-up on the anterodorsal area of the specimen as in Figure 42, arrow indicates lunular incision, length of section 0.95 mm.



Figures 40–43. Small specimens from the ‘Canyon River site,’ note that the posterior branch of the bifurcating cardinal 3b is more detached from 3a than in the larger specimens shown above. Figure 40. Close-up on hinge of left valve, length of section 2.1 mm (USNM 534959). Figure 41. Close-up of hinge of right valve, length of section 2.0 mm (USNM 534960). Figure 42. Left valve of articulated specimen, length 5.3 mm (USNM 534961). Figure 43. Close-up on the anterodorsal area of the specimen as in Figure 42, arrow indicates lunular incision, length of section 0.95 mm.

Formation in California, USA (Squires & Gring, 1996); the original *Vesicomya tschudi* is from outcrops in the upper Oligocene (Chattian) 'Pleurophopsis zone' in the Heath Formation in northern Peru, which have recently been identified as hydrocarbon seeps (Kiel & Peckmann, in press).

Archivesica knapptonensis Amano & Kiel, sp. nov.

(Figures 30–43)

Calyptogena (*Calyptogena*) *chinookensis* Squires & Goedert. Goedert & Squires, 1993:74, fig. 4.

Diagnosis: A small-sized *Archivesica* with elongate shell sculptured by fine irregular concentric lines and with short anterior cardinal tooth in right valve.

Holotype: Fragment of right valve with preserved hinge dentition, length 13.5 mm+, height 7.0 mm, USNM 534954.

Paratypes: USNM 534956, fragment of left valve with preserved hinge dentition, length 19.0 mm+, height 11.0 mm; USNM 534956, fragment of left valve with preserved hinge dentition, length 11.0 mm+, height 7.0 mm; LACMIP 12097, fragment of right valve with hinge dentition, length 8.8 mm.

Type locality: LACMIP loc. 5843, beach terrace of the Columbia River near Knappton, Washington State, USA; upper Oligocene part of the Lincoln Creek Formation.

Description: Shell small, elongate and little inflated; escutcheon elongate and narrow; lunular incision well developed, elongate; postero-dorsal margin almost straight, angulate at transition to pointed posterior margin; ventral margin straight or slightly convex, anterior margin pointed but evenly rounded. Sculpture of irregular commarginal growth lines only. Pallial line pallial line starting at postero-ventral end of anterior adductor scar, not discernable in posterior part of shell. Right valve hinge with thick, blunt middle cardinal (1), slightly concave, subparallel to shell margin, its posterior half situated below anterior cardinal (3a); anterior cardinal (3a) very short, thin, parallel to shell margin; posterior cardinal (3b) bifurcate, pointing in a postero-ventral direction. Left valve with moderately thick, straight anterior cardinal (2a) parallel to shell margin; middle cardinal (2b) very thick, peg-like, pointed at its posterior side; posterior cardinal (4b) elongate, slightly thinner than 2a, slightly convex, pointing in a postero-ventral direction. Subumbonal pit oval and well developed in right valve, much smaller in left valve. Nymph elongate, about twice as long as hinge tooth area. Anterior adductor scar moderately deep impressed, pear-shaped. Anterior pedal retractor

scar deeply impressed, positioned between anterior cardinal tooth and anterior adductor scar.

Comparison: As far as we know, this is by far the most elongate fossil *Archivesica*. The Recent Japanese *A. laubieri* (Okutani & Metivier, 1986) is similar to *A. knapptonensis* in having an elongate outline, fine irregular concentric lines, and a thin anterior cardinal tooth (3a). *Archivesica laubieri* has a much larger shell and a shorter nymph than *A. knapptonensis*. Another Recent Japanese species, *Archivesica tsubasa* Okutani, Fujikura & Kojima, 2000 is even more elongate than *A. knapptonensis* and has a similarly long nymph. It differs from *A. knapptonensis* by the complete absence of a lunular incision, a very short cardinal 3a and a non-bifurcating cardinal 3b in the right valve. *Archivesica tsubasa* also grows to a much larger size (up to 212 mm in length) than any of the fossil specimens reported herein. The type species *A. gigas* differs from *A. knapptonensis* in having a broader, less elongate shell, a proportionally shorter nymph, the cardinal tooth 2b of the left valve has a broader base, and cardinal tooth 3b of the right valve is slightly concave and does not appear to bifurcate.

Distribution: Upper Oligocene cold seep deposits of the Lincoln Creek Formation, Washington State, USA.

Etymology: After the vanished town of Knappton near the type locality. Knappton was founded by Jabez B. Knapp soon after the end of the U. S. Civil War and first thrived on a cement plant that most likely used seep limestone. Later the town was supported by timber. It had a post office from 1871 to 1941, and rapidly declined after the sawmill burned down in 1941.

Archivesica georgemoorei Amano & Kiel, sp. nov.

(Figures 44–49)

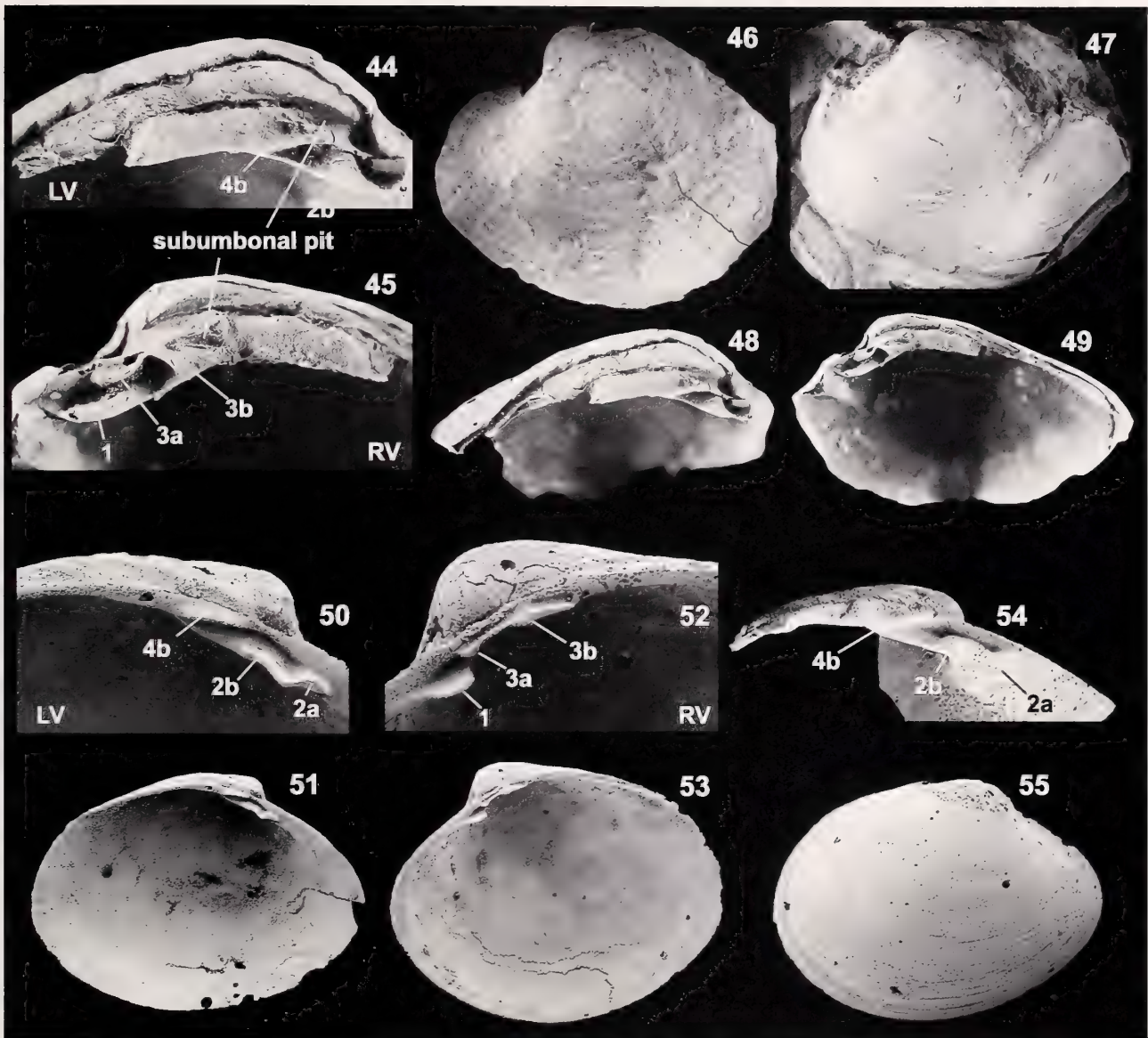
“new genus of Vesicomidae” Moore, 1969:A32.

Diagnosis: A medium-sized *Archivesica* with oval shell and with very short anterior cardinal tooth in left valve.

Holotype: Internal mold, length 46 mm+, height 35 mm, UCMP 55517, we figure rubber casts of each valve.

Paratypes: Six specimens from the type locality (USGS loc. M1755), figured specimens include UCMP 55519 (left valve, length 48.5 mm, height 43.0 mm), and UCMP 55520 (left valve, length 48.0 mm, height 38.0 mm).

Type locality: USGS loc. M1755; about 300 m below the top of the Sitkalidak Formation in the type area at 57°11.1'N, 152°56.6'W, on the north shore near the



Figures 44–49. *Archivesica georgemoorei* n. sp. from the Sitkalidak Formation on Sitkalidak Island, Alaska, USA (USGS loc. M1755), all specimens coated with ammonium chloride. Figures 44–45, 48–49. Rubber casts of the holotype, UCMP 55517. Figures 45, 49. Right valve, length 47.0 mm. Figures 44, 48. Left valve, length 35.0 mm. Figure 46. Paratype, UCMP 55519, external view of left valve, length 48.5 mm. Figure 47. Paratype, UCMP 55520, external view of left valve, length 48.0 mm.

Figures 50–55. *Isorropodon frankfortensis* n. sp. from the Astoria Formation in Washington State, USA (USGS loc. M2790), all specimens coated with gold for SEM photography. Figures 50–51. Paratype, interior of left valve and close-up of hinge, length 3.2 mm (USNM 534962). Figures 52–53. Holotype, interior of right valve and close-up of hinge, length 3.3 mm (USNM 534963). Figure 54. Left valve hinge of a fragment of a large specimen, length 1.6 mm (USNM 534964). Figure 55. Exterior of a right valve, length 3.5 mm (USNM 534965).

east end of Sitkalidak Island, Alaska; Oligocene(?) part of the Sitkalidak Formation.

Description: Shell medium size, oval and moderately inflated; beak prominent, prosogyrate, slightly anterior of midline; escutcheon present; sculpture of weak irregular commarginal growth lines only, no postero-

dorsal ridge. Hinge moderately broad, teeth positioned below to slightly anterior of umbo. Right valve hinge with strong, elongate ventral cardinal (1) parallel to hinge margin, its posterior half situated under anterior dorsal cardinal (3a); anterior dorsal cardinal (3a) thin, elongate, slightly concave, subparallel to antero-dorsal margin; posterior dorsal cardinal (3b) rather thick,

bifid, pointing in a postero-ventral direction. Left valve hinge with long, thin, and slightly convex posterior cardinal (4b) pointing in a postero-ventral direction; above middle cardinal it seems to fuse with what could be the anterior cardinal (2a); middle cardinal (2b) stout, slightly pointed on anterior side. Nymph almost as long and broad as hinge teeth area; subumbonal pit present in both valves. Pallial line unknown.

Comparison: This species was reported as ‘a new genus of Vesicomysidae’ by Moore (1969) but had never been described in detail. We think that the species can comfortably be placed in the genus *Archivesica* because it has a hinge dentition and subumbonal pit similar to the type species *A. gigas*. However, *A. georgemoorei* differs from other *Archivesica* species by its almost straight cardinal 1 in the right valve that runs parallel to the shell margin, in most other *Archivesica* species the posterior end of cardinal 1 points upwards to the beak. This feature also distinguishes *A. georgemoorei* from the type species. In addition, *A. gigas* has a higher cardinal 2b.

Distribution: Known only from the type locality.

Etymology: After the late Dr. George W. Moore (Corvallis, Oregon), who collected and first reported these shells.

Genus *Isorropodon* Sturany, 1896

Isorropodon Sturany, 1896:17.

Type species: *Isorropodon perplexum* Sturany, 1896 (by monotypy); Recent, north of Alexandria, eastern Mediterranean Sea.

Remarks: Cosel & Salas (2001) wrote that *Isorropodon* is distinguished from *Vesicomys* by its much larger and more oval to oval-oblong shell, the poorly developed or missing lunular incision, and the smooth valve margin without an incision. *Vesicomys* is smaller, the shells are very tumid to nearly spherical, and the general hinge-teeth configuration is the same. However, two of these ‘distinguishing’ characters appear to be not very distinctive. The lunular incision of *Vesicomys* was diagnosed by Cosel & Salas (2001) as very weak to well-defined, thus there seems to be little difference between ‘very weak’ (as in *Vesicomys*) and ‘poorly developed’ (as in *Isorropodon*). Also the difference in size appears to be gradual rather than distinctive: *Vesicomys* ranges from 3 to 13 mm in length, *Isorropodon* from 11.3 to 47 mm in length. The major difference between the two genera, and the reason why we keep them separate, is the ctenidium, which has two demibranchs in *Vesicomys*, but only one in *Isorropodon*. *Callogonia* has a similar shell outline but can easily be distinguished from *Isorropodon* based on its posterior area, its

obliquely truncate posterior margin, and the presence of a deep pallial sinus.

Isorropodon frankfortensis Amano & Kiel, sp. nov.

(Figures 50–55)

Diagnosis: A small *Isorropodon* with smooth and ovate shell, anterior margin slightly pointed; central cardinal 3a in right valve straight, very long, parallel to dorsal shell margin, nymph very narrow; lunular incision indistinct or absent.

Holotype: Length 3.3 mm, height 2.7 mm, USNM 534963.

Paratype: Length 3.2 mm, height 2.4 mm, USNM 534962.

Type locality: USGS loc. M2790, near Frankfort on the north shore of Columbia River, Wahikaikum County, Washington State, USA; lower Miocene part of the Astoria Formation.

Description: Shell small, attaining 10.5 mm in length, ovate and moderately inflated; beak prosogyrate, slightly elevated, in subcentral position; no lunular incision. Shell surface smooth with very fine growth increments. Hinge plate narrow, right valve with cardinal 1 just anterior of beak, thin, elongate, and parallel to dorsal shell margin; cardinal 3a commencing just below anterior margin of beak, elongate and very thin, slightly thickened anteriorly, parallel to dorsal shell margin, bends slightly ventrally at its posterior end; cardinal 3b just posterior of 3a and equally thin, slightly oblique toward dorsal shell margin, dipping down at the posterior side. Left valve: Cardinal 4b thin, subparallel to dorsal shell margin, 2a and 2b fused, slightly thicker than 4b but still thin, posterior part (presumably 2b) convex, anterior part (presumably 2a) slightly thicker, pointing slightly dorsally. In larger specimens, 4b more ventrally inclined and thicker, 2a and 2b shorter, more compact, and much thicker. Pallial line and sinus indistinct.

Comparison: Cosel & Salas (2001) reviewed and redescribed the Recent Atlantic species of *Isorropodon* in great detail. *Isorropodon perplexum* is the most similar species in shell outline and hinge features; the hinge dentition on the left valve is virtually indistinguishable from that of *I. frankfortensis*, the dentition of the right valve of *I. frankfortensis*, however, has thinner, more elongate, and more strongly fused posterior cardinals (3a and b). *Isorropodon bigoti* Cosel & Salas, 2001 has a similar shell outline but the hinge area is higher, and the teeth are more narrowly spaced and more strongly developed than in *I. frankfortensis*.

Isorropodon curtum Cosel & Salas, 2001 from off Mauritania is less elongate than *I. frankfortensis*, and *I. striatum* (Thiele & Jaekel, 1931) has internal striation and an exterior posterior ridge which are not visible on *I. frankfortensis*. This new species is not only the first certain record of *Isorropodon* from outside the Atlantic Ocean, but also the first fossil record of the genus. A fossil shell with similar external outline is *Callocardia* (*Agriopoma*) *californica* Clark, 1918, from the Oligocene San Lorenzo Formation of middle California (Clark, 1918). But with a length of 49 mm, that species reaches a much larger size than *I. frankfortensis*, and its hinge dentition is clearly veneroid rather than vesicomysid (Clark, 1918, pl. 11, fig. 11).

Distribution: Cold-seep carbonates in the lower Miocene part of the Astoria Formation along the north shore of the Columbia River, Washington State, USA.

Etymology: After the vanished town of Frankfort near the type locality. Frankfort had a post office from 1890 until 1918; in 1947 the population had decreased to 11 residents, and in 1960 only two inhabitants remained.

Genus *Pliocardia* Woodring, 1925

Pliocardia Woodring, 1925:147.

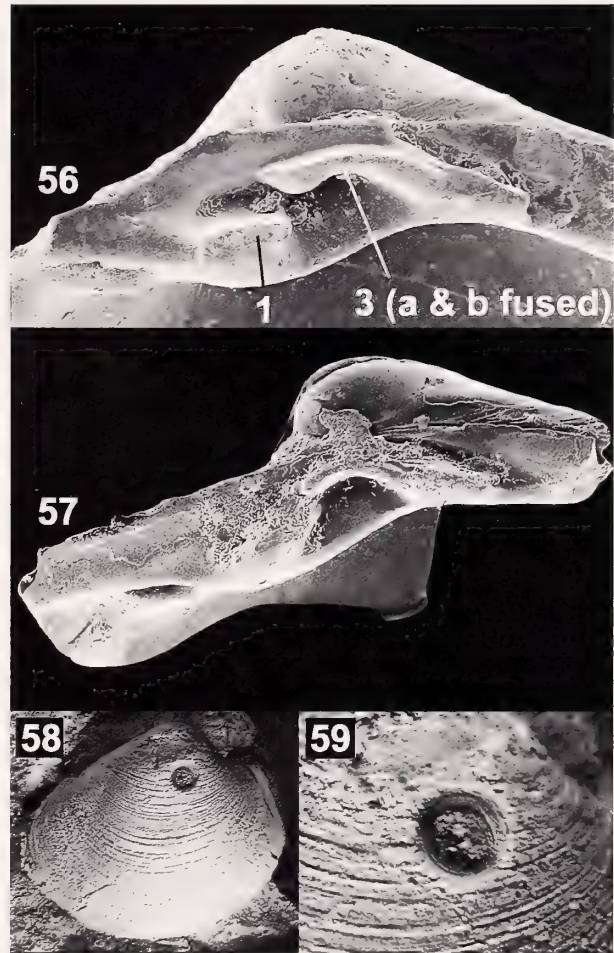
Type species: *Anomalocardia bowdeniana* Dall, 1903 (by original designation); Miocene, Jamaica.

Remarks: Woodring (1925) pointed out similarities between *Pliocardia* and *Vesicomya* regarding shell size, the lunule, and the similar arrangement of dentition. However, *Pliocardia* differs from *Vesicomya* by having thicker shells and a much thicker posterior cardinal tooth. The dentition of *Pliocardia* is, in fact, closer to that of *Archivesica* (see Figure 5). However, *Pliocardia* has a shorter anterior cardinal tooth in each valve, and lacks a subumbonal pit. Krylova & Janssen (2006) suggested that the Recent Japanese '*Vesicomya*' *crenulomarginata* Okutani, Kojima & Iwasaki, 2002 represents a living member of *Pliocardia*.

Pliocardia? sp.

(Figures 56–59)

Description: Shell oval in outline, with fine commarginal growth increments only; umbo subcentral, slightly prosogyrate. Hinge of right valve with elongate, moderately strong anterior cardinal (1) parallel to dorsal shell margin, positioned just anterior below beak; central cardinal (presumably fused 3a and b) moderately strong, convex; anterior end peg-like, thickened, positioned below beak; central part somewhat constricted; posterior part slightly thicker, paral-



Figures 56–59. *Pliocardia*? sp. from upper Oligocene seep deposits of the Lincoln Creek Formation, Washington State, USA. Figure 56. Right valve hinge, from the 'Canyon River site,' length 1.5 mm, USNM 534966. Figure 57. Another right valve hinge from the same locality, length 1.9 mm (USNM 534967). Figures 58–59. Specimen with a hole most likely drilled by a naticid from the Satsop River (LACMIP loc. 17747b), length 6.0 mm (USNM 534968).

lel to postero-dorsal shell margin. Deep groove between cardinal 3 and the thin nymph.

Material and Distribution: Four specimens from Oligocene seep carbonates in the Lincoln Creek Formation, Washington State, USA.

Remarks: The few available shells of *Pliocardia*? sp. from the 'Canyon River site' in Washington State are so fragile that complete shells could not be recovered; only hinges of the right valve are known. The dentition closely resembles that of the Miocene type species *Pliocardia bowdeniana* from Jamaica, thus we tentatively assign our specimens to this genus. A small specimen (7 mm long) with the same general outline as

Table 3

Range chart of vesicomylid genera treated herein. Dashed line indicates questionable occurrence.

Genus	Age	l. m. ~ l. Eocene	Oligocene	e.~m. Mio.	l. Miocene	Recent
<i>Archivesica</i>		—————	—————	—————	—————	—————
<i>Hubertschenckia</i>		—————	—————	—————	—————	—————
<i>Adulomya</i>		—————	—————	—————	—————	—————
<i>Calyptogena</i>		—————	—————	—————	—————	—————
<i>Isorropodon</i>		—————	—————	—————	—————	—————
<i>Pliocardia</i>		—————	-----	—————	—————	—————

Pliocardia? sp. but unknown hinge dentition from another Oligocene seep site in the Lincoln Creek Formation (LACMIP loc. 17747b, see Kiel, 2006 for details) has a parabolic hole with an inner diameter of 0.6 mm and an outer diameter of 0.9 mm. This hole was most likely drilled by a naticid. This is the first record of a chemosymbiotic bivalve in a cold seep with a drill hole in North America. Peckmann et al. (2002) reported naticids with drill holes from a seep site in the Lincoln Creek Formation but none of the bivalves from that site show drill holes (Peckmann et al., 2002; own observation). When Amano & Jenkins (2007) described drill holes in upper Eocene cold-seep bivalves from Hokkaido, they suspected that the Lincoln Creek Formation naticids could not cope with the presumed chemical deterrent in the soft tissue of these cold-seep bivalves (cf. Kicklighter et al., 2004), based on Peckmann's observation. However, considering the drilled *Pliocardia*? sp. reported here, it is necessary to reexamine this hypothesis.

REMARKS ON CRETACEOUS VESICOMYIDS IN JAPAN

Three vesicomylid species have been reported from Cretaceous strata (Albian to Campanian) of Japan, and these three species account for the apparent discrepancy between molecular age estimates and the geologic record of the family, as mentioned in the introduction (cf. Little & Vrijenhoek, 2003). Internal features like hinge dentition and pallial line of these species, however, have never been sufficiently examined.

When Kanie & Sakai (1997) illustrated small (= about 33 mm) elliptical specimens as *Calyptogena* (*Ectenagena*) sp. from the Albian Middle Yezo Group near Mikasa City, central Hokkaido, they did not describe the hinge structure and probably identified it only based on shell outline and surface sculpture. We

examined a fair number of newly collected specimens from this locality, all of which are present as internal molds (steinkerns), but none of them shows scars of their putative hinge dentition. As we have shown herein, such scars are often present in steinkerns of Cenozoic vesicomylids. Moreover, *Calyptogena* (*Ectenagena*) sp. at this site is associated with many solemyid specimens that are similar in size to *Calyptogena* (*Ectenagena*) sp. These solemyids show a considerable range of shell shapes and ornamentation, some of which resemble that of *Calyptogena* (*Ectenagena*) sp. as figured by Kanie & Sakai (1997). Thus we find it likely that this *Calyptogena* (*Ectenagena*) sp. is in fact a solemyid.

Hikida et al. (2003) illustrated a large bivalve from the 'Omagari seep site' of the Santonian to Campanian Upper Yezo Group near Nakagawa Town in northern Hokkaido as *Calyptogena* sp. They did not illustrate its hinge structure, thus its vesicomylid affinities can not be confirmed.

A large fossil bivalve (the holotype is 130 mm long) was described as *Vesicomya inflata* Kanie & Nishida, 2000, from the Cenomanian of the Middle Yezo Group in northwestern Hokkaido. The fossil locality consisted of two large carbonate concretions found as float in the river bed of the Sanjussen-zawa (Kanie et al., 2000). The available material at the Yokosuka City Museum consists of two articulated specimens (R. G. Jenkins, personal communication 2006), thus its hinge dentition could not be examined. Moreover, this species would be very large for *Vesicomya* (cf. Cosel & Salas, 2002), and has a deeply impressed asymmetrical lunule, a feature that can sometimes be seen in lucinids, but not in vesicomylids. In summary, the hinge dentition of all three of these Cretaceous vesicomylids proposed to date is unknown, and thus their vesicomylid affinities are uncertain.

Table 4

Fossil North Pacific vesicomysids not discussed here because additional material was not available.

Species	Occurrence	Age	Status
<i>Adulomya</i> (?) <i>azarie</i> Shikama, 1969 [in Shikama & Masujima, 1969]	Japan	Pliocene	No hinge data
<i>Akebiconcha kawamurai elongata</i> Ozaki, 1958	Japan	Pliocene	Considered as <i>Archivesica</i>
<i>Calyptogena (Adulomya) uchimuraensis</i> <i>kurodai</i> Kanno & Tanaka, 1998 [in Kanno et al., 1998]	Japan	middle Miocene	Synonym of <i>Adulomya</i> <i>uchimuraensis</i> Kuroda, 1931
<i>Calyptogena akanudaensis</i> Tanaka, 1959	Japan	middle Miocene	No hinge data
<i>Calyptogena bosoensis</i> Kanie & Kuramochi, 2001	Japan	Pliocene	Hinge data insufficient
<i>Calyptogena</i> (?) <i>gibbera</i> Crickmay, 1929	California	early Pliocene to middle Pleistocene	Considered as <i>Archivesica</i> (herein)
<i>Calyptogena lasia</i> Woodring, 1938	California	early Pliocene to middle Pleistocene	Synonymized with <i>C. gibbera</i> by Squires (1991) but considered valid by Krylova & Janssen (2006)
<i>Calyptogena moraiensis</i> Suzuki, 1941	Japan	late Miocene	Synonymized with <i>C. pacifica</i> Dall, 1891 by Otatume (1942)
<i>Calyptogena nipponica</i> Oinomikado & Kanehara, 1938	Japan	late Miocene to Pliocene	Hinge data insufficient
<i>Calyptogena panamensis</i> Olsson, 1942	Costa Rica/ Panama	late Miocene or early Pliocene	Considered as <i>Calyptogena</i> by Krylova & Sahling (2006)
<i>Lamelliconcha kawadai</i> Aoki, 1954	Japan	early to middle Miocene	Similar to <i>Issoropodon</i> (outline) and <i>Waisiuconcha</i> (dentition)
<i>Solemya (Adulomya?) hachiyai</i> Nomura, 1935	Japan	late Miocene	No hinge data
<i>Vesicomya ellipsoidea</i> Kanie & Kuramochi, 2001	Japan	Pliocene	Hinge data insufficient

DISCUSSION

With the exclusion of the doubtful Cretaceous vesicomysids discussed above, the oldest confirmed vesicomysid is *Archivesica* cf. *tschudi* from cold seeps in the late middle Eocene (Table 3). *Adulomya chinookensis* and *Hubertschenckia ezoensis* appeared more-or-less simultaneously in the late Eocene. During the Oligocene, a species potentially belonging to *Pliocardia* appeared in cold seeps in the northeastern Pacific Ocean along with *Isoropodon* in the early Miocene, with *I. frankfortensis* also at cold seeps. *Adulomya* started to colonize whale-falls in the Miocene, with *A. chitanii* in the early Miocene (Amano et al., 2007) and the apparently whale-fall endemic species *A. hokkaidoensis* in the middle Miocene. These findings have several interesting implications. The proposed discrepancy between molecular age estimates [21.5–43.8 Ma according to Peek et al. (1997)] and first fossil occurrences of vesicomysids [ca. 106 Ma according to Kanie & Sakai (1997)] as emphasized by Little & Vrijenhoek (2003) disappears with the removal of vesicomysids from the Cretaceous record. The earliest vesicomysids with confirmed vesicomysid-type hinge architecture occur approximately between 36–38 Ma and are thus well within the range indicated by molecular estimates (Peek et al., 1997; Baco et al.,

1999). Considering that already three distinct genera were present at that time, the last common ancestor of the modern vesicomysids lived earlier than that, but probably not much earlier.

The 'stepping stone' hypothesis predicted that vesicomysid bivalves (among other taxa) underwent a significant radiation once whale falls were inhabitable for them (Baco et al., 1999; Smith & Baco, 2003). Kiel & Goedert (2006) showed that vesicomysids did not occur at whale falls during the Eocene and Oligocene but only from the Miocene onward, and they suggested that the early whales had too little oil in their bones to sustain seep- or vent-like chemosynthetic ecosystems. However, they did not preclude the possibility that vesicomysids underwent a major radiation once they started to adapt to whale-falls in the Miocene. But our new data does not seem to support this possibility either. The first radiation among vesicomysids took place long before their first appearance at fossil whale falls, as indicated by the presence of three large-shelled vesicomysid genera (e.g., *Adulomya*, *Archivesica*, and *Hubertschenckia*) at cold seeps in the Eocene and Oligocene. Although *Calyptogena* and *Isoropodon* first appear in the Miocene, these genera have not been found so far at Miocene whale falls. Four to five vesicomysid species have been reported from modern whale falls (*Archivesica gigas*, *Adulomya elongata*,

Calyptogena pacifica?, and the *Archivesica soyoe-kilmeri* complex; cf. Naganuma et al., 2001 and Smith & Baco, 2003) which are from a broader range of genera than in the Miocene. Although we were not able to revise all known vesicomysid species from the North Pacific (see Table 4), the presently available data shows little evidence for any correlation between the evolution of whales and of vesicomysids, at least in this region. Admittedly, these suggestions are hampered by the scarcity of fossil whale falls, and even fossil cold seeps, in other parts of the world.

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Note added in proof: Dr. George Moore, after whom *Archivesica georgemoorei* is named, was unexpectedly killed in an auto accident on Oct. 4, 2007.

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Middle Miocene Chemosynthetic Thraciid *Nipponothracia gigantea* (Shikama, 1968) from Central Japan is a Large Lucinid Bivalve (Lucinoidea: Mollusca)

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Abstract. *Nipponothracia* Kanie & Sakai, 1997, a recently proposed bivalve genus with the type species *Thracidora gigantea* Shikama, 1968 from the middle Miocene of central Japan, was previously regarded as amongst the largest in Thraciidae and only the member in this family which participates in fossil cold-seep assemblages. We found and examined a large specimen referable to *N. gigantea* in the collection of National Museum of Nature and Science, Tokyo, which reveals that *N. gigantea* belongs to Lucinidae. The genus *Nipponothracia* still remains as a distinct genus of Lucinidae due to its remarkable shell characters; nevertheless its familial position changed drastically from Thraciidae to Lucinidae. *Nipponothracia ponbetsensis* Kanie & Sakai, 1997 from the Albian of northern Japan and *Thracia yezoensis* Kanie & Kuramochi, 1996 from the Cenomanian of northern Japan are also large lucinids referable to *Nipponothracia*, but their positive assignment to that genus awaits better preserved specimens. *Nipponothracia* is a candidate for generic identification of poorly known, large and edentulous lucinid bivalves from Mesozoic and Cenozoic cold-seep assemblages.

INTRODUCTION

Three specimens of a large bivalve from the Miocene of Japan were originally described as *Thracidora gigantea* and placed in the anomalodesmatan family Thraciidae (Shikama, 1968). These specimens were collected from the upper part of the Morito Formation (now remapped as Oyama Formation by Eto et al., 1998) of the Hayama Group at a cliff (now destroyed) near the northern exit of a road tunnel in Higashi-hayami [*sic*] (= Higashi-hemi), Yokosuka City in Miura Peninsula, central Japan. Research Group for Giant Clam Communities of the Hayama Group (1995) mentioned an additional occurrence of this species from the Hayama Group at Ikegami about 300 m southeast of the type locality in the same city, where it was found associated with a cold-seep chemosynthetic molluscan assemblage (Kanie et al., 1995b; Kanno & Kanie, 1995; Naganuma et al., 1995). Later, Kanie & Sakai (1997) established the new genus *Nipponothracia* on the basis of *T. gigantea* as the type species, along with a description of a new species *Nipponothracia ponbetsensis* from the upper Albian (Cretaceous) of

Hokkaido, northern Japan. Kanie & Sakai (1997) regarded *N. ponbetsensis* as a member of an Albian chemosynthetic community. The two *Nipponothracia* species are the only examples of the family Thraciidae in chemosynthetic communities (see Majima et al., 2005; Kiel & Little, 2006).

However, interpretation of *Nipponothracia* as belonging to Thraciidae by these authors is open to question. Thraciids have a posteriorly directed (opisthogyrate) beak, an edentulous hinge, a posterior external ligament, a pallial sinus, granular shell surface, etc. The most difficult point to agree on is the position of the ligament within the shell. Shikama (1968:15) correctly described the ligament groove located behind the hinge plate (therefore posterior) but this structure is positioned along the antero-dorsal instead of the postero-dorsal margin, assuming that it belongs to Thraciidae. This ligament groove is clearly observable in one of the two illustrated syntypes (Shikama, 1968, pl. 2), which was later designated as the lectotype by Kanie & Sakai (1997). Kanie & Sakai (1997), in contrast, suggested that the ligament is small and positioned along the postero-dorsal margin (see Kanie

& Sakai, 1997 fig. 2). However, we could not find any structure in the posterior hinge plate indicative of the presence of ligament in the lectotype. They did not mention the groove that Shikama (1968) described as the ligament. These authors stated that the right valve is more convex and smaller than the left. However, the "left" valve is slightly crushed by sediment compaction, so that it is still uncertain whether or not the shell is inequivalve in *N. gigantea*. Goedert et al. (2003) already suggested that this species actually belongs to Lucinidae. However, the crucial evidence of this has never been provided. Therefore, documentation of additional reliable shell characters is indispensable to ascertain the systematic position of this interesting bivalve.

We here report additional shell characters of *N. gigantea* based on a specimen stored in the National Museum of Nature and Science, Tokyo and show that *N. gigantea* belongs to Lucinidae.

MATERIAL AND LOCALITY

The specimen described here is in the collection of the National Museum of Nature and Science, Tokyo with registration number NSM PM11610, which was identified as *Schizothaerus keenae* Kuroda and Habe (*Tresus* in current generic assignment), a mactrid bivalve common in modern shallow waters and younger Pleistocene shallow-marine beds in Japan. The label attached to this specimen indicates that the specimen was collected by late Dr. Hiroshi Ozaki (a previous director of the Department of Geology, National Science Museum, Tokyo) on September 15, 1952. The label also indicates that the specimen was obtained from 'Miocene Amatsu mudstone' and cites 'Tenjinyama junior high school, Nashizawa, Kimitsu County' as the collection site. The place name is now in the southern part of Futtu City in Boso Peninsula, Chiba Prefecture. 'Tenjinyama junior high school' seems to be the collection site of this specimen, and it seems that it was incorrectly recorded for a branch school of Tenjinyama elementary school once located in Nashizawa and closed in 1967 (Figure 1).

Younger Cenozoic forearc-basin sedimentary rocks in the Nashizawa area comprise the underlying Kinone Formation and overlying Amatsu Formation with either conformable or in fault contact each other; both belong to the Awa Group of Middle Miocene age (Nakajima and Watanabe, 2005). Both formations in this area consist mainly of massive mudstone deposited at lower to middle bathyal depths (Saito, 1992), so that it is difficult to confirm from which formation NSM PM11610 derived on the basis of its matrix alone. A nannofossil analysis of the matrix from NSM PM11610 with light microscopy, identified heavily over-calcified, poorly preserved nannofossils with derived forms from late Oligocene through early Miocene rocks. In the

matrix, *Sphenolithus heteromorphus*, which identifies the base of zone CN3 and the top of CN4, are abundant, and other nannofossils indicative of middle Miocene age are totally absent. Therefore, the age of NSM PM11610 can be estimated in the range between 18.1 and 13.6 Ma (Okada & Bukry, 1980; Backman et al., 1990). The Kinone and Amatsu formations on the Boso Peninsula have been dated as 16–13 Ma and 13–5 Ma, respectively, by micropaleontological, fission track and K-Ar isotope datings (Oda, 1977; Mita & Takahashi, 1998; Motoyama & Takahashi, 1997; Watanabe & Takahashi, 1997; Takahashi & Danhara, 1997; Kameo et al., 2002). Therefore, it is highly probable that NSM PM11610 was derived from the Kinone Formation. Our extensive survey in the Nashizawa area found neither additional specimens nor any chemosynthetic assemblages in the Kinone Formation. We are tempted to assume that NSM PM11610 is a solitary occurrence in the formation.

The collecting site of NSM PM11610 is located on the opposite side of Tokyo Bay and about 25 km east-southeast of the type locality of *N. gigantea*. The Hayama Group in the Miura Peninsula is an accretional complex in origin and is the western extension of the Hota Group on the Boso Peninsula, on which the Kinone Formation overlies unconformably. Microfossil analyses demonstrate that the Hayama Group exposed at Ikegami is early Middle Miocene (ca. 15 Ma) and deposited in the middle bathyal zone (Aita, 1995; Akimoto et al., 1995; Kanie & Asami, 1995; Okada, 1995; Taketani, 1995). It is highly probable that the Hayama Group at the type locality is also early Middle Miocene in age because both localities are in same stratigraphic unit and located only 300 m apart. Therefore, NSM PM11610 is almost equivalent to the lectotype in age despite both fossil-bearing beds being of different tectonic origin (see also Kanie et al., 1991).

SYSTEMATIC PALEONTOLOGY

Family LUCINIDAE Fleming, 1828

Genus *Nipponothracia* Kanie & Sakai, 1997

Type species: *Thracidora gigantea* Shikama, 1968: Middle Miocene, central Japan.

Diagnosis: Shells very large (up to ca. 220 mm long), sub-elliptical and longer than high, weakly inflated, moderately thin-shelled, anterior margin more broadly rounded than posterior one, with surface ornamented only by rugose growth lines. No escutcheon and lunule. Hinge plate edentulous, arched, with a shallow concavity below beak and a shallowly sunken dorsal ligament. Umbones not prominent, located well anterior to vertical midline, only slightly bent anteri-

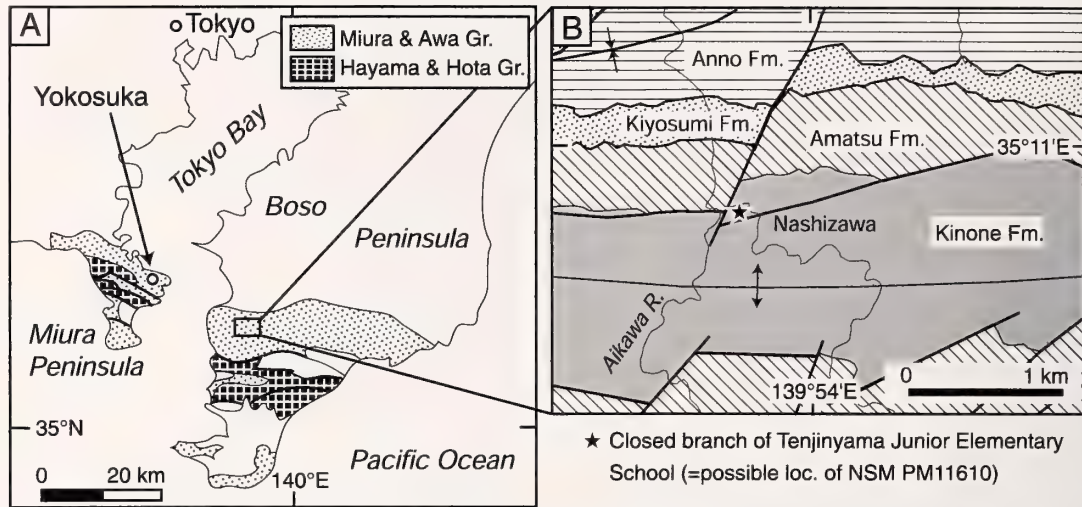


Figure 1. (A) Geologic sketch map of the Boso and Miura Peninsula. (B) Geologic map around the fossil locality of NSM PM11610 (modified after Nakajima & Watanabe, 2005).

orly. Anterior adductor scar moderately short and thick, as long as posterior one, dorsally diverging from pallial line for half of its total length. Posterior adductor scar large and elliptical. Valve inner margin smooth.

Nipponothracia gigantea (Shikama, 1968)

(Figures 2–8)

Thracidora gigantea Shikama, 1968:14, pl. 2, figs. 1–3; text-fig. 1.

Thraciidae (gen. nov.) *gigantea* (Shikama). Kanie et al., 1995a:66, fig. 4.

?*Thracia kakumana* (Yokoyama). Kanie et al., 1995a:66, fig. 4.

Nipponothracia gigantea: Kanie & Sakai, 1997:210, fig. 5.

Type material: Lectotype, designated by Kanie & Sakai, 1997, YCM-GP. Ig01A, in Yokosuka City Museum, Yokosuka. Two paralectotypes, not found but seemingly in the collection of Yokohama National University.

Type locality: Higashiemi 4-chome, Yokosuka City, Miura Peninsula, central Japan (35°16'09"N, 139°38'50"E, see Kanie & Sakai, 1997:fig. 1).

Description: The description here is based on the lectotype (Figure 2) and NSM PM11610 (Figures 3–8). Both specimens exhibit a similar state of preservation in that the shells are fragmented into many pieces and some shell pieces subside into the matrix by compaction as to even the surfaces of shell and internal mold to the same level. This is particularly evident in the right valve of NSM PM11610. In addition to this,

the left valve is dislocated anteriorly more than 10 mm from the right valve, so that the anterior margin of the left valve is missing, although NSM PM11610 consists of conjoined valves.

The shell is unusually large and moderately thin for a lucinid. NSM PM11610 may attain ca. 220 mm long if the lost posterior shell margin is complete, and 150 mm high and ca. 80 mm thick (joined valve), which is about 1.5 times larger than the lectotype. Although Shikama (1968) and Kanie & Sakai (1997) described the lectotype as inequivalve (the right valve is more convex than the left in their interpretation), NSM PM11610 is evidently equivalve (Figure 3). This disagreement between the two specimens is likely to be due to sediment compaction for the lectotype. The outline, well seen in the lectotype, is elliptical, inequilateral, with a height/width ratio of 7.7. The umbones are situated well anterior to the vertical midline, bend weakly forward, and protrude only slightly beyond the dorsal margin. The anterior margin is much more narrowly rounded than the posterior one, the anterodorsal margin is almost straight, and the ventral margin is broadly and evenly rounded, without any angulation between the anterior and posterior margins. The shell exterior is ornamented entirely with rugose concentric growth lines, and, in NSM PM11610, with two, faint, axial ribs extending from the umbones to the anterior margin.

The hinge plate, seen only in the lectotype (Figure 2), is moderately narrow and arched with a narrow ligamental nymph behind the beak, thin and short in front of the beak, and is edentulous only with a shallow notch below the beak. The lunule and escutcheon are absent.

The features of the shell interior are seen only in NSM PM11610 (Figures 4–8). The anterior adductor

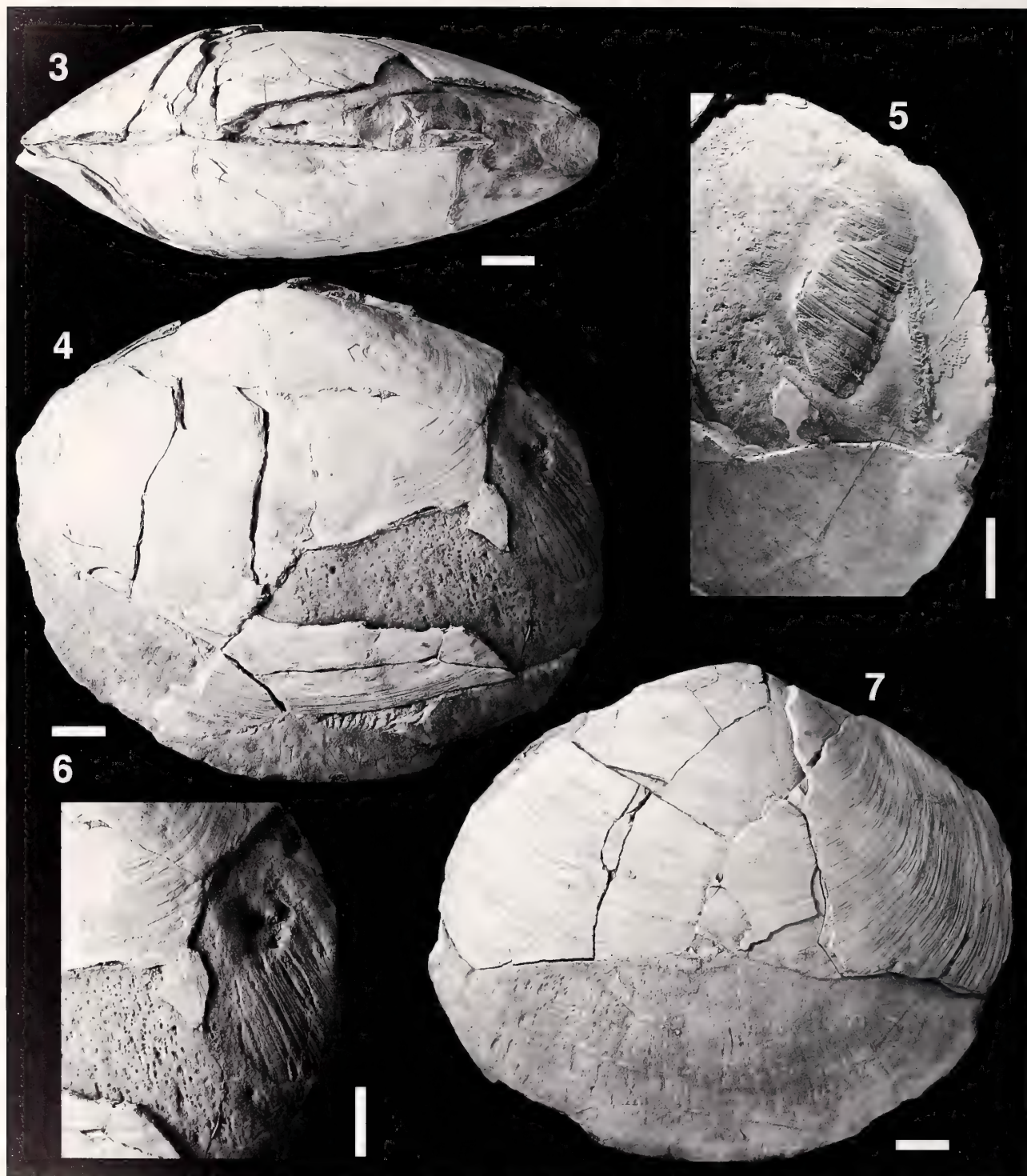


Figure 2. *Nipponothracia gigantea* (Shikama), lectotype, YMC-GP Ig01A, in the collection of Yokosuka City Museum, Yokosuka. Scale bar 10 mm.

scar, clearly visible on the inner mold of the right valve, is short, as long as the posterior adductor scar, broad, and truncated obliquely at the distal end, with irregular striae. The posterior adductor scar, visible on the inner mold of the left valve, is large and elliptical. The pallial line is obscure in most part due to abrasion of the inner mold, but is clearly seen near the anterior adductor scar that diverges dorsally from the pallial line for slightly more than the half of its total length. The inner shell surface has many radial striae near the ventral margin and its ventral edge is smooth. No trace of the pallial blood vessel can be seen on the internal mold.

DISCUSSION

Our detailed observation on NSM PM11610 demonstrates that *Nipponothracia gigantea* is unequivocally a member of Lucinidae because it has the adductor muscle scars and pallial line typical of Lucinidae: the anterior adductor scar is more enlarged than the posterior one and detached from the lines of pallial attachment scars for slightly more than half of its total length. Previous assignment of *N. gigantea* to Thraciidae is therefore due to the absence of the information on the shell interior in the type specimens as well as the



Figures 3–7. *Nipponothracia gigantea* (Shikama), NSM PM11610 in the collection of National Museum of Nature and Science, Tokyo, specimen coated with ammonium chloride. Figure 3. Umbonal view. Figure 4. Left valve. Figure 5. Inner mold of the anterior muscle adductor scar in the right valve, photographed after removal of shell. Figure 6. Inner mold of the posterior muscle adductor scar in the left valve. Figure 7. Right valve. Scale bars 20 mm.

incorrect interpretation of shell orientation and features.

Although the systematic position of *N. gigantea* has changed drastically from Thraciidae to Lucinidae, *Nipponothracia* is likely to survive as a genus even within the Lucinidae. Lucinidae have traditionally been classified into four subfamilies, Lucininae, Myrteinae, Milthinae and Divaricellinae (Chavan, 1969). Bretsky (1976) proposed a different scheme of classification, and recognized seven groups within the family based on North American Cenozoic forms without suprageneric categories. A recent molecular phylogenetic analysis using 18S and 28S rRNA genes has provided results that are incongruent with the previous classifications by shell morphology as well as exclusion of Thyasiridae and Ungulinidae from Lucinoidea (i.e., non-monophyly of Lucinoidea) and inclusion of *Fimbria* (only the modern member of Fimbriidae) within the Lucinidae (Williams et al., 2004). Taylor & Glover (2006) stated that it is at present premature to erect a new classification without developing rigorous studies of molecular and morphological analyses. Therefore, it would be unwise to discuss the subfamilial position of *Nipponothracia* at present.

The only species confidently assignable to *Nipponothracia* at present is *Lucina (Miltha) hetzeli* Martin, 1933 from the late Oligocene asphalt bed in Buton, Indonesia (see also Beets, 1943). The Buton asphalt bed was recently revised by Janssen (1999) as a late Miocene in age (Tortonian to Messinian). *L. (M.) hetzeli* has overall shell characteristics similar to *N. gigantea* except for its much smaller shell size. One of us (TK) recently found several specimens referable to *L. (M.) hetzeli* from an early Pliocene cold-seep assemblage in northwestern Leyte, Philippines. The largest and seemingly adult specimen attains 91 mm in length. There is a possibility that *N. gigantea* is a junior synonym of *L. (M.) hetzeli*, but the final decision requires additional material and studies.

Kanie & Sakai (1997) included a large bivalve (*N. ponbetsensis*) in a seep-related chemosynthetic association from the early Late Albian deposit in the Mikasa area of central Hokkaido, Japan to *Nipponothracia*. The shell characteristics of this species are, according to their description, represented by oval shell shape, concentric surface ornamentation, absence of a lunule and escutcheon, and edentulous hinge, which match well with *N. gigantea*. In addition to these characters, we observed the presence of a long ligamental nymph posterior to the beaks and the absence of the purported "posterior ligament" by those authors. Although the muscular nature is not known, this species appears to belong to Lucinidae. Kanie & Kuramochi (1996) described *Thracia yezoensis*, another large bivalve in a possibly seep-related association from the Cenomanian deposit of the Obira area, northwestern Hokkaido,

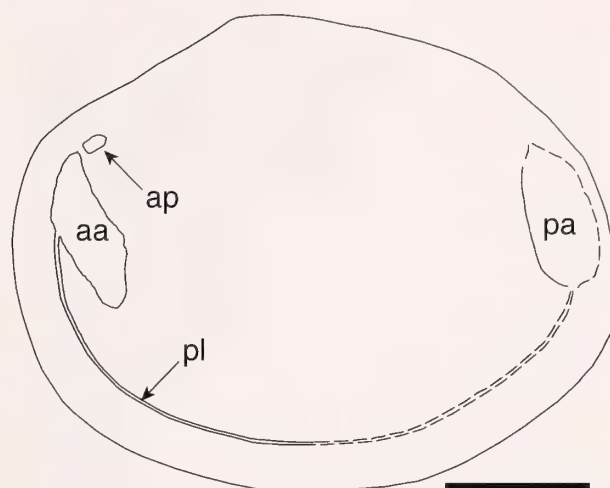


Figure 8. Semi-schematic drawing of the muscle scars and pallial line in *Nipponothracia gigantea* (Shikama) based on NSM PM11610. Right valve. Abbreviations: aa, anterior adductor muscle scar; ap, anterior pedal retractor muscle scar; pa, posterior adductor muscle scar; pl, pallial line. Scale bar 50 mm.

Japan (see also Kanie et al., 1996). This species has almost the same shell characteristics as *N. ponbetsensis*, being seemingly congeneric and even conspecific with *N. ponbetsensis*. We found an internal mold of this species, which was collected by Y. Shigeta of the National Museum of Nature and Science, Tokyo from the type locality of *T. yezoensis*. This specimen reveals the presence of an elongate anterior muscle adductor scar that is more elongate than the posterior one and seemingly detached from the pallial line, supporting an allocation to Lucinidae instead of Thraciidae. Hikida et al. (2003) recorded bivalves probably assignable to *N. ponbetsensis* within a Santonian or Campanian fossil cold-seep community in the Upper Yezo Group of Nakagawa area, northern Hokkaido, Japan. Allocation of these Cretaceous forms from Hokkaido to *Nipponothracia* requires further study to clarify the characteristics of the shell interior for generic determination as well as more specimens for species comparisons.

Several large (sometimes giant) lucinids with edentulous hinge plates have been reported from modern and fossil cold-seep and normal shallow marine assemblages. These are *Meganodontia* Bouchet & Cosel, 2004, *Cryptolucina* Saul et al., 1996, *Bulacanites* Kase & Aguilar, 2007, and *Hadrulucina* Woodring, 1982. *Meganodontia* was described as a monotypic genus, and its type species *M. acetabulum* Bouchet & Cosel, 2004 attains 150 mm in length and is from bathyal depths off Taiwan, most probably of cold-seep in origin. We found a fossil example of this species from an early Pliocene cold-seep assemblage in Leyte, Philippines (unpublished). *Bulacanites* also accommo-

dates only the type species *B. obtusiplicatus* Kase & Aguilar, 2007, attains 120 mm in length and is from the middle Pliocene intertidal to subtidal shallow marine sediment in Bulacan province of central Luzon, Philippines. Kase & Aguilar (2007) suggested that the world largest lucinid *Lucina megameris* Dall, 1901a (see also Dall, 1901b; Cox, 1941), which attains 290 mm in length and 280 mm in height in the largest specimen (Cox, 1941) and was assigned to *Phacoides* (*Pseudomiltha*?) by Dall (1901b:829) and questionably to *Eomiltha* by Bretsky (1976:290), belongs to *Bulacanites*. Both *Meganodontia* and *Bulacanites* differ from *Nipponothracia* in their circular shell outline and strongly prosogyrous umbones. *Hadrulucina* accommodates the type species *Anodontia? angustana* Gardner 1951 from the middle Eocene Tallahatta Formation of the southeastern United States and *Hadrulucina zenica* Woodring (1982) from the Miocene La Boca Formation in Panama. These species were suggested to be shallow marine dwellers (Saul et al., 1996:791). Although the muscular-scar patterns and detailed hinge structures are unknown, *H. angustana* has thin, almost equilateral valves and swollen umbones like *Anodontia*, and is therefore distinct from *Nipponothracia*.

The only lucinid genus with a large shell and edentulous hinge resembling *Nipponothracia* is *Cryptolucina*, which includes the type species *C. megadyseides* Saul et al., 1996 and *C. ellasodyseides* Saul et al., 1996, both from cold-seep assemblages in the middle to late Eocene Hamptulips Formation, western Washington, USA (Saul et al., 1996). Another species referable to *Cryptolucina*, as already suggested by Majima et al. (2005) and Kase & Aguilar (2007), is *Saxolucina* (*Megaximus*) *matsushitai* Matsumoto, 1971 from the lower Miocene Setogawa Group in central Japan. *S. (M.) matsushitai* has strongly prosogyrate and protruding umbones above the dorsal shell border and coarse concentric lamellar growth lines, which are quite similar to *C. megadyseides*. *Cryptolucina* clearly differs from *Nipponothracia* in having strongly prosogyrate umbones, concave antero-dorsal margin and coarse concentric lamellar growth lines. *C. ellasodyseides*, on the other hand, is not so typical of *Cryptolucina* as it has a more elongate shell outline and weakly prosogyrate and seemingly inconspicuous umbones. These shell characters are rather similar to *Nipponothracia*. However, *C. ellasodyseides* is unique as it has radial swellings both in the anterior and posterior parts with a slight median depression in the shell surface, which is not known in *C. megadyseides* and *N. gigantea*. A final decision on the generic position of *C. megadyseides* is deferred until rigorous revision of Mesozoic large lucinid-like bivalves is undertaken. Kelly et al. (2000) described another new species, *Cryptolucina kuhnpasetensis* from the late Barremian seep-related limestone mounds in Northeast Greenland. This species is very

similar to *N. gigantea* in shell form and in muscular and ligamental features. We suggest that *C. kuhnpasetensis* is similar to *Nipponothracia* rather than to *Cryptolucina*.

Saul et al. (1996) and Kelly et al. (2000) enumerated many examples of large and seemingly edentulous bivalves possibly referable or similar to *Cryptolucina* from the Mesozoic and Cenozoic formations, mostly of cold-seep in origin, of which '*Lucina*' *colusaensis* Stanton (1895:pl. 11, figs. 4, 5) from the Upper Jurassic and Upper Cretaceous Knoxville Beds, California is an additional species comparable to *Nipponothracia*. However, the hinge and muscle-scars are totally unknown for this species (Saul et al., 1996:791). In addition to this, a large bivalve reported by Gill et al. (2005:fig. 7C) as 'lucinid B' from the Miocene Freeman's Bay Limestone, Trinidad is similar to *N. gigantea* in having a laterally expanded oval shell. These cannot be assigned properly to *Nipponothracia* without detailed descriptions on the hinge and muscle-scars.

This study demonstrates that no Thraciidae have yet been found associated with cold-seep chemosynthetic assemblages. Although Lucinidae are not common in modern cold-seep chemosynthetic communities probably due to the difficulty of sampling with the submersible manipulator (e.g., Sibuet & Olu, 1998), they are a major group of bivalves found associated with cold-seep assemblages in the Cenozoic and Cretaceous in Japan (see Majima et al., 2005).

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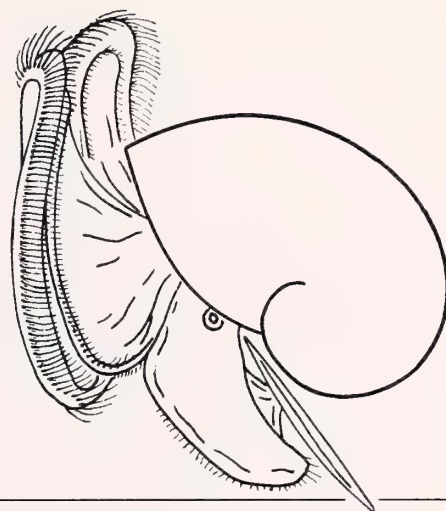
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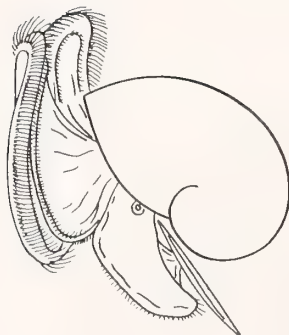
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